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# Comparative Anatomy Within the Genus *Euonymus*.

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THE family of Celastraceæ (Lindl.) contains about 38 genera, with 375 species of trees and shrubs, many of whoch are climbing. It is distributed throughout both hemispheres excepting in the Arctic zones.

Just where and when the family originated is very uncertain according to the available papers on this subject, but it is thought probable that it had its origin in Europe and was distributed in Europe and North America during the Cretaceous periods. During the Tertiary times the family, and especially the genera *Euonymus* and *Celastrus,* is thought to have been distributed not only in Europe and North America but as far as Greenland, Spitzbergen, Alaska, Australia and Java. The paleontological findings have been mostly leaves. The present-day distribution of the Celastraceæ, and in particular of *Euonymus* and *Celastrus,* lends support to the belief that the Celastraceæ were to be found in both Europe and North America during Tertiary times. Of the species of *Euonymus* living to-day, *E. europœus* and *E. latifolius* are known in the Quaternary strata from Europe.

Rehder lists only five out of the thirty-eight genera of the Celastraceæ as occurring in North America. The following notes concerning these five genera are taken from his "Manual of Cultivated Trees and Shrubs":

"*Euonymus:* About 120 species, in North and Central America, Europe, Asia and Australia.

"*Celastrus:* More than thirty species in eastern and southern Asia, Australia and America.

"*Pachistima:* Two species in North America.

"*Glossopetalon:* Three or four species in North America.

"*Tripterygium:* Three species in eastern Asia."

Because of their great ornamental value, these trees and shrubs have been under cultivation for a long time, a fact which makes it difficult to trace their distribution, or even, in fact, to know their native habitat in many instances.

Concerning the general distribution of *Euonymus,* the following is quoted from Sargent: "The Sylvia of North America," Volume 2:

"The genus *Euonymus* is widely distributed through the Northern Hemisphere, extending south of the equator to the islands of the Indian archipelago and to Australia. Botanists now distinguish about forty species, the largest number occurring in the tropical regions of southern Asia, in China and in Japan. Several species are found as far south as the mountains of Ceylon. One of the Indian species occurs also in Sumatra and in Java, and one species has been detected in northern Australia.

"The genus is represented in central Asia and is widely scattered with a number of species through the Orient and through temperate and southern Europe. In North America two species occur in the Atlantic and one in the Pacific regions and three or four little-known species inhabit southern Mexico."

This paper will deal with nine species of *Euonymus.* This genus contains about 120 species, according to Rehder. He describes twenty-three species and a number of varieties as occurring in North America. In "Standardized Plant Names" only fourteen species and three varieties are listed for North America.

With the exception of *E. radicans,* all of the species studied are shrubs or small trees. They are easily recognized by the fruit. The next most marked field character is the four ridges in the bark, which is characteristic of most species. The stems are usually green, due to the persisting assimilatory tissue.

The following is a list of the species which are to be discussed in this paper. They represent, as far as is known to the writer, all of the available species to be found growing in this immediate locality. Rehder's "Manual of Cultivated Trees and Shrubs" has been used quite freely in writing the following brief descriptions. The dates of introduction are those given in the manual. Concerning these dates the following general explanation is quoted from Rehder's introduction:

"Most of the foreign trees and shrubs and even some native ones have reached our gardens by the way of Europe, and it is only within the last fifty years that, chiefly through the agency of the Arnold Arboretum, many plants have been introduced from their native country, mostly from eastern Asia, directly to American gardens. Lack of space forbids to give in this book details regarding the introduction, and only the year, if known, is given; when this could not be ascertained, the first record of the plant as being in cultivation is given, based either on the mention in horticultural literature

or on dated herbarium specimens. As the most complete and reliable records regarding the introduction of plants into cultivation are found in English horticultural literature, most dates, particularly those of older introductions, refer to England, though in many cases the plants may have been in cultivation earlier on the continent of Europe or in this country."

## *Euonymus alatus* Reg.

Winged Shrub.

Introduced 1860. Its native habitat is given as Japan, Korea, Manchuria and China.

This is one of the most easily recognized of all shrubs because of its unique cork wings, which grow out wedge-shaped along four sides of the stem. It is a more or less spreading shrub, growing to a height of eight feet. The branches are stiff with two to four (usually four) broad, corky wings. The leaves are short-stalked, elliptic or obovate, acute at both ends, finely and sharply serrate, one to two inches long.

## *E. americanus* L.

Strawberry Bush; Brook *Euonymus*.

Introduced 1683. Habitat from New York south to Florida and west to Texas.

It is an upright shrub, six to eight feet high, easily recognizable in the late summer by its very numerous small clusters of fruit, which remind one of strawberries. The leaves are lance-ovate to lanceolate, one to three inches long, acuminate, cuneate, crenate-serrate, dark green in color.

## *E. atropurpureus* Jacq.

Wahoo; Burning Bush.

Introduced 1756. Native from New York to Florida, west to Minnesota, Nebraska, Oklahoma and Texas.

A treelike shrub growing from six to as much as fifteen or eighteen feet high. It has a more or less fluted ash-gray bark on the older stems; the twigs vary from green to plum color. The leaves are elliptic or ovate-elliptic, acuminate, serrulate, pubescent beneath, one and one-half to five inches long. The petioles are one-third to two-thirds of an inch in length. The fruit is about a half inch across and matures in October. "The purple husk parts and reveals the seed, enveloped in a scarlet outer coat that fits it loosely. The delicate pale lining of the purple envelope makes harmony between the two stronger colors, and the plum-colored twigs and yellow leaves contribute to make this indeed a burning bush, that glows brighter as the advancing winter opens all the husks and displays the scarlet seeds. No brighter dash of color can be added to gardens or shrubbery borders than this tree, which shows its beauty chiefly in the dead of winter."

### *E. bungeanus* Maxim.

Winterberry.

Introduced 1883. Native of China and Manchuria.

A shrub or small tree to fifteen feet high with slender branches. The leaves are elliptic-ovate to elliptic-lanceolate, two to four inches long, long-acuminated, broad cuneated at the base, finely serrate with petioles up to almost an inch in length.

### *E. europaeus* Linn.

Spindle Tree; European Burning Bush.

In cultivation for a long time. A native of Europe to western Asia.

An erect shrub or sometimes a small tree to twenty feet high. The leaves are elliptic-ovate to lance-oblong, from one and a half to two and a half inches long, acuminate, cuneate, crenate-serrate, petiole up to half an inch in length.

### *E. europaeus nanus* Lodd.

Dwarf Burning Bush.

Origin and introduction unknown.

This is a dwarf, dense and strictly upright form with elliptic to elliptic-lanceolate leaves from one to one and a half inches long or on vigorous shoots to two and a half inches long. No fruit has ever been produced by the plants which were studied for this paper.

### *E. maackii* Rupr.

Cultivated since 1880. Native of north China, Manchuria and Korea.

Large shrub or small tree; leaves are glabrous, elliptic-oblong to lance-oblong, acuminate, gradually narrowed toward the base, serrulate, two to three inches long and three-fourths to one and one-fourth inches broad. The petioles are one-sixth to one-fifth as long as the leaves.

### *E. patens* Rehd.

The Spreading *Euonymus*.

Introduced about 1860. Native of eastern and central China.

A half evergreen or nearly evergreen spreading shrub to ten feet. The lower branches procumbent and sometimes rooting, the branchlets obscurely four-angled, minutely warty. The leaves are elliptic to elliptic-oblong, rarely obovate-oblong, acute, cuneate at the base, crenately serrulate, bright green above.

### *E. radicans* Sieb.

Winter Creeper.

Introduced 1865. Native of north and central Japan and Korea.

A low procumbent shrub, with often trailing and rooting or climbing branches, climbing sometimes to twenty feet. Branches are terete, densely and minutely warty. The leaves are roundish to elliptic-oval, rounded or narrowed

at the base, crenately serrate, usually dull green above with whitish veins; one-half to two inches long. According to Schenck: "In Japan it climbs as an evergreen shrub in light places, especially on evergreen trees, and in the Japanese woods it takes the place of the less abundant ivy to a certain extent."

Of the above group, *E. atropurpureus* is the only species growing wild in this vicinity. Specimens of this species were collected from four different sources: From the timber on Botany Bluff, two or three miles east and north of Lawrence. From Gage Park at Topeka; some of the plants there had been obtained from the government, others were growing wild. From the timber near Mr. Bunker's cabin, seven miles south and west of Lawrence. A lawn in Lawrence; this plant had been brought in from the timber and replanted.

*E. alatus and E. bungeanus* specimens were obtained at the Mt. Hope Nurseries near Lawrence. There were about twenty-five individuals of *bungeanus* and between fifty and a hundred of *alatus*.

*E. americanus, patens, radicans, europaeus nanus,* and *maackii* were all collected from Gage Park. Most all of these had been obtained originally from the government, but it was impossible to get exact information concerning them. Definite information concerning the immediate genetic relationship of individuals would have been very helpful in attempting to explain several peculiarities which have appeared during the course of this study.

*E. europaeus* is growing on the University campus.

The most inclusive work that has been done on the genus *Euonymus* is that of Stenzel (*18*). He studied the leaf and stem of some seventeen species and made a key for the species studied. The key was based on the histological structures of the leaf and petiole. His material was chiefly herbarium specimens. The species he studied were *E. pauciflora, nanus, velutinus, atropupureus, alatus, occidentalis, angustifolius, japonicus, fimbriatus, pendulus, verrucosus, garcinoides, latifolius, europaeus, scandens, tarmentosus* and *japanicus*.

Metz (*8*) has fully described the leaf of *E. alatus, americanus* and *europaeus*.

Petit (*11*), discussing the occurrence of fat bodies in the assimlatory tissue, says that no great degree of systematic value can be attributed to their occurrence. With the fat bodies Petit also classes the small caoutchouc bodies which are to be found in some species. These caoutchouc bodies have been made the subject of two papers. Col (*2*) described their occurrence in a number of species, *E. japonicus, fimbriatus, radicans, nanus, europaeus, latifolius, americanus,*

*verrucosus, alatus,* and in the root of *atropurpureus.* He concluded that they are generally present in the cortex, in the phloëm region of the stem and also of the root, although the cells secreting them do not appear in all species at the same age. In most species they do not occur until the stem is at least two years old, and in *E. alatus* they do not occur excepting in very old branches. He considered the secretions to be lactiferous, having some properties characteristic of caoutchouc. He did not find these secretions in the leaf blade, petiole, pith or cortical parenchyma. Metz (*8*), on the other hand, found what is probably this caoutchouc in the epidermal cells around the stomata, in the palisade cells and in special containing cells in the leaf of *E. alatus,* but not in *E. americanus* or *europaeus.*

Möeller (*9*), in an examination of the cortical region of *E. obovatus* (*E. americanus*), *latifolius,* and *verrucosus,* found in *obovatus* "compact worm-formed fibers" which it is presumed are the cells secreting the caoutchouclike substance. He considered them to have arisen by a "mucilaginous or pectin metamorphosis of certain bast fibers." Col (*2*), on the other hand, says that "he is completely mistaken in their nature inasmuch as he considers them as fibers in the process of pectic transformation."

The cells described by Möeller were present in the specimen of *americanus* studied for this paper. Their walls were slightly thicker than most of the parenchyma cells of the cortex, and in shape they are blunt-ended tubes. It seems more likely that they are simply modified parenchyma cells. The caoutchouclike substance was quite abundant in a four-year-old stem, occurring not only in these particular cells but also in other short parenchyma cells of the phloëm, and also in the thin-walled parenchyma cells inside of the assimilatory tissue. The same substance was found in the same regions in *E. radicans* and also in the cells of the outer cylinder of the collenchyma and occasionally in a medullary ray cell and in pith cells which were near the outer margin. In *E. patens* some of the parenchyma cells just outside of the phloëm contained caoutchouc. In the other species studied there was no indication of it.

Concerning the origin of the bark there are differences of opinion. Möeller (*10*) states that the epidermis forms the phellogen in the species which he studied. Solereder (*16*), quoting Stenzel (*18*), says the cork arises in the epidermis throughout *Euonymus.* Weiss (*19*) briefly states his findings in connection with cork formation in *E. alatus, latifolius* and *europaeus* as follows:

"Cork formation begins in the epidermis, where the outer walls are very much thickened. At first a phelloderm cell is cut off, then a cork cell toward the outside, which cell in *europaeus* and *alatus* constitute the complete cork layers in the two-year-old stem. The wings in *alatus* are cork formation composed of cells strongly stretched radially."

Gregory (*4*), in her study of *E. alatus, europaeus,* and three varieties of *europaeus—variegatus, ovatus* and *purpureus,* found in *E. europaeus purpureus* cork originating from the collenchyma cells immediately below the bundles of bast fibers at the corners of the stem. In *alatus* she says:

"The first indication of it externally is a little line of brown flecks at equal distances from the ridges at the corners. They may easily be mistaken for lenticels, but on examination they are found to be the first stages of the wing, which originates directly from the stomata. . . . It is well known that *E. verrucosus* has warty projections of cork which are said to arise from lenticels, though at the time of their origin there is no appearance of periderm, unless the outer cylinder, which we have described as collenchymatic cells, be considered periderm."

Concerning the little brown flecks of bark, etc., Stahl (*17*) says that these are not lenticels and that their origin is in no way connected with the stomata, but that they are rather corky outgrowths of the cortical parenchyma which elevates the epidermis.

Quoting from Stenzel (*18*):

"Von Höhnel describes the phellem of *E. europeus* very precisely. He describes four cork wings and cork masses lying between. The latter are very irregularly developed, in some places strongly, in others little or none at all. They consist of alternate layers of phelloid of varying thickness and true cork. The four cork wings are strong and consist for the most part of phelloid layers, which are the first thing formed each year, and consist of hard, brown-walled, radially elongated cells containing one or more red-brown clumps which are lacking in the cork cells. The three to four layers of cork cells which regularly alternate with the phelloid are quite small."

From the present studies it would seem that the origin of the cork is variable in the different species. In *E. europaeus nanus* it arises form the epidermis (pl. XXIV, Fig. 2). An epidermal cell divides first radially and then in the direction of the circumference. The inner cells then divide in the direction of the circumference of the stem and produce cork cells on the outside, and by the further production of these cork cells the epidermal layer is shoved out until it splits, resulting in a "little brown fleck" of bark which resembles a lenticel in appearance. These brown flecks increase in number, grow in size and unite with each other until eventually the stem is covered with a thin, rough bark.

The origin of the wings in *alatus* was found also to be epidermal (Pl. XXIV, Fig. 4). A cell is cut off from the epidermal cell, this cell then divides, producing a cork cell on the outside and itself becoming a phellogen cell.

In *E. americanus* the first indication of cork is at the four corners of the stem during the first season's growth. Here it is formed by the cells of the collenchyma cylinder inside of the epidermis (Pl. XXIV, Fig. 1, c-c).

It is also derived from the collenchyma in *E. atropurpureus* and *europaeus*. In *atropurpureus* bundles of bast fibers are always present at the corners of the stem, but within the collenchyma layers (as described later). The collenchyma cells around this bundle produce a ring of corklike cells completely surrounding these fibers, but more abundant toward the inner side. By their continued production the epidermis is broken and a weakly developed and temporary (as compared with *alatus*) cork wing arises (Pl. XXIII, Figs. 10, 11, 12, 13).

Gris (*5*), according to Stenzel, was the first to investigate the availability for taxonomy of the anatomical condition of the pith. On the basis of his results he established three types:

1. Homogeneous pith, consisting of living cells (thick-walled and starch-bearing) with or without crystal sacs.
2. Heterogeneous pith, consisting of living and of empty cells, the latter usually thin walled.
3. Empty pith, consisting of empty cells only.

Kasner (*6*) studied the large peculiar cavities in the pith and decided they were simply the results of tearing of the thin walls during growth by the large cluster crystals of calcium oxalate.

The purpose or purposes of this study have been to determine if the species characters are as clearly marked throughout all or any of the internal tissues as they are in the external structures, so that keys could be made for species identification based on the variations found in the tissues; to ascertain if some tissues are more variable than others, and if so to account for the differences; and to find out whether or not species which have been developed in geographically isolated regions differ from each other more than those which have been developed in the same general regions.

Cross and longitudinal sections as well as mascerations of the stem were studied from both fresh and preserved material. These studies were chiefly made from the fifth and sixth nodes from the last terminal bud scars of the two-year stems, although the fourth or

fifth node of the one-year stem was also examined. The sections were cleared and detailed drawings were made at uniform magnifications. The leaves were studied from the surfaces and from sectioned material. The petioles were sectioned.

Where measurements are given they are the result of an average of at least ten cells and usually from two to three different pieces of material.

In the species studied it was impossible to definitely recognize an endodermis. Therefore, as is customary, all tissues from the epidermis to the phloëm will be called primary cortex. The secondary cortex will be considered as all tissues produced by the cambium toward the outside and all tissues of the periderm.

## THE STEM.

### *E. atropurpureus* Jacq.

The cells of the epidermis as seen in cross section are strongly arched, almost pointed on the outer side, and flat on the inner side, giving them a somewhat triangular shape (Plate XXII, Fig. 1). The radial diameter of the cell is 19.9 microns and the diameter at the base is 12.9 microns. The outer wall of the epidermis is usually comparatively thin, 7 microns, and is never equal to one-half of the radial diameter of the cell in thickness. Stomata are fairly numerous, they are sunken and have air spaces below.

Beneath the epidermis is a layer of clear collenchymalike cells. These cells have their long axes in the direction of the circumference of the stem. They are about twice as long as wide, being about as long as the epidermal cell is wide. This layer varies from two cells to three, four or even five cells in thickness at short intervals, resulting in a wavy or wrinkled appearance of the epidermis. At four nearly equidistant points these cells cut through the layer next beneath them and connect with another collenchymalike layer. Thus there are two cylinders of collenchymalike tissue connected with each other at four points, which will be termed the corners of the stem (Pl. XXIII, Fig. 1).

Between the two cylinders of collenchyma tissue there is a layer four or five cells thick of nearly isodiametric thin-walled cells which contain chloroplasts. These assimilatory cells in *atropurpureus* contain fewer chloroplasts than any other species studied, possibly due to the purplish pigment in the epidermis.

Toward the end of the first year, or during the early part of the second year of growth, cords of bast fibers are found at the corners of the stem in the collenchyma which connects the two collenchyma cylinders. These cords develop by differentiation and a thickening of the walls of the collenchyma cells in a region of tissue connecting the two cylinders just beneath the line of the outer cylinder (Pl. XXIII, Fig. 10). Differentiation continues until at times as many as seventy-five or eighty bast fibers are formed. Collenchyma cells completely surround this bundle of fibers. As growth continues the bundles are shoved outward, resulting in ridges on the stem. These ridges

connect the outer angles of the leaf scars as shown in plate XXIII, figure 13. Toward the end of the second year the ring of collenchyma cells around the bast fibers produce corklike cells toward the inside, *i. e.*, immediately around the bast fibers (Pl. XXIII, Fig. 11). This proliferation is much greater on the inner side than on the outer (Pl. XXIII, Fig. 12). The epidermis is broken and sloughed off and the bast bundle is shoved to the outside, where it is gradually sloughed off along with the cork cells as new cork is formed. These cork lines are unquestionably derived from the collenchyma cells. The portions of the epidermis between the ridges remain intact into the third and fourth years except for thin, long patches which gradually grow larger and become more numerous until the entire stem is covered by a thin cork. By this time all indications of the original ridges of cork have disappeared.

Next inside of the inner collenchyma cylinder thin-walled parenchyma cells extend in to the phloëm region. These cells are all larger than the collenchyma cells, those nearer the phloëm being the largest. These large cells form a more or less continuous ring. They measure as much as 62 microns by 31 microns in cross diameter. Between these and the phloëm there is an irregular layer of much smaller parenchyma cells. Their walls are somewhat thicker than those of the other parenchyma cells. They are always so wrinkled that it is impossible to get accurate measurements of their size. Roughly, they are 1/6 to 1/8 the size of the larger cells just mentioned and from four to six times the size of the phloëm cells. In longitudinal sections they are seen to be short, blunt-ended tubes. Between the phloëm and the parenchyma are occasional solitary thick-walled bast fibers.

Cluster crystals of calcium oxalate are fairly numerous in the parenchyma, but they are also found in the other tissues of the cortex. Since their occurrence is variable and seemingly dependent on habitat, and possibly seasonal conditions of the plant, it is not considered that they have much systematic significance.

The cells of the phloëm in cross section are small and thin-walled, rectangular in shape and regular in size. They appear to be more or less marked off in squares by the medullary ray cells in the radial direction and by small parenchyma cells in the tangential direction. These cells are about four times as long as wide when seen in longitudinal sections.

The xylem consists chiefly of tracheal tubes, tracheids and wood fibers. The wood fibers frequently more or less encircle the larger tubes and are by far the most abundant elements of the xylem.

The medullary rays are one cell in thickness. The cells are flattened as seen in cross sections, while in longitudinal radial sections they vary. Some are square, some have their long axis in the radial direction and others have their long axis in the vertical direction (Pl. XXIV, Fig. 6). There are from four to six rays in an arc of 175 microns at the circumference of the xylem.

The pith cavity is roughly almost square in the two-year-old stem, although it is more rounded in the one-year-old stem, the four corners being at points alternate with the corners of the stem. The pith cells are empty, with the exception that some contain large clustered crystals of calcium oxalate, and are very thin-walled. They are usually torn out in sectioning. Starch is not stored in the pith.

## *E. europaeus* Linn.

The epidermal cells are arched on their outer surface, but are more flattened than in *atropurpureus,* measuring 12.6 microns in their radial diameter and 23.1 microns in their tangential diameter. The outer wall of the epidermis is slightly thicker than in *atropurpureus,* 8.75 microns, and its surface conforms to the upper margin of the cavity (Pl. XXII, Fig. 2).

The collenchymatic tissue, as in *atropurpureus,* consists of two cylinders connected at the four corners and separated, excepting at the corners, by assimilatory tissue. The cells of this assimilatory tissue are small and rounded, their long axis in the direction of the circumference. Chloroplasts are very abundant, giving the stem a bright green color excepting at the four corners, where the absence of chlorophyll results in a whitish line. For the most part the stem is predominantly green for at least three years, frequently longer. The outer cylinder of collenchyma is quite uniformly two cells thick, consequently the epidermis has a smoother contour in contrast with the wavy or wrinkled condition in *atropurpureus.* The development of the walls of the collenchyma cells is much weaker than in *atropurpureus.* This is especially true of the inner cylinder, where frequently these cells merge into the thin-walled parenchyma layer beneath so gradually that it is difficult to distinguish the dividing line.

On stems of rapid growth bundles of bast fibers followed by lines of cork formation at the corners may or may not develop. In slow-growing stems they do not occur. The bundles of bast fibers, if present, never exceed twenty to twenty-five cells in number, usually fewer. The cork forms a considerable ridge at times, but generally it is sloughed off almost as rapidly as it is formed.

The parenchyma tissue in the cortex of *europaeus* is quite similar to that of *atropurpureus,* as are also the phloëm and xylem tissues. Occasional solitary bast fibers occur between the parenchyma and the phloëm.

The medullary rays are one cell thick. There are four to five of them in an arc of 175 microns at the outer edge of the xylem in the two-year stem (Pl. XXIV, Fig. 7).

The pith cells are empty excepting for clustered crystals. They are very thin-walled and are easily torn out, as in *atropurpureus.* The pith cavity in the one-year-old stem of *europaeus* is diamond-shaped, less than twice as long as broad in cross section, the ends of the diamond being rounded and protruding (Pl. XXIII, Fig. 2).

## *E. bungeanus* Maxim.

The most noteworthy difference between *bungeanus* and *atropurpureus* is in the size of the cells. The corresponding tissues bear the same relationships to each other.

The epidermal cells have their long diameter in the direction of the circumference. They measure 30.8 microns by 19.9 microns. The outer wall of the epidermis measurers 10.5 microns in thickness. The epidermal cells are only slightly arched on their outer sides (Pl. XXII, Fig. 3.

The outer cylinder of collenchymatic tissue is composed of cells which are larger and more irregular in size and shape than in *atropurpureus.* The walls of the cells at the four corners are more thickened than elsewhere. No bundles

of bast fibers develop at the corners but, usually not before the third year, cork ridges are formed which are similar in every way to those already described for *atropurpureus* and *europaeus*. The cells beneath these ridges become greatly stretched, seeming to indicate that growth was taking place more rapidly in all other parts of the cortex.

The assimilatory tissue is composed of rather uniformly large cells which are very abundantly supplied with chloroplasts.

The thin-walled parenchyma inside of the inner collenchyma cylinder is similar to that of the other species, excepting for the size of the cells. These measure as much as 28 by 56 microns. Bast fibers are found, solitary or in groups of two or three, in the layer of small parenchyma cells next inside of these large ones. In the great majority of stems these bast fibers are very scarce, but occasionally a stem is found in which they are quite abundant.

The medullary rays are a single cell in width (Pl. XXIV, Fig. 8). They average five in 175 microns at the outer margin of the xylem.

The pith is heterogeneous. Most of the cells have comparatively thin walls, but thicker than in *europaeus*. The cells are not uniform in size and do not contain stored starch or calcium oxalate crystals. The pith cavity in the one-year-old stem is diamond-shaped, but is much smaller in proportion to the size of the stem than in any other species studied excepting *alatus* (Pl. XXIII, Fig. 3).

## *E. maackii* Rupr.

The epidermal cells are almost triangular in shape. Their average size is 21.4 microns in both the radial and the tangential diameters. The thin outer wall, 7 microns in thickness, is strongly arched. The epidermis remains intact as long as five or six years.

The collenchyma cylinders have their cell walls strongly thickened, especially so at the corners of the stem where the two cylinders are connected. The cells are quite regular in size and shape and give the cortex a very compact appearance (Pl. XXII, Fig. 4).

No bast fibers develop at the corners, nor is there any indication of cork-wing formation.

The cells of the assimilatory tissue are regular in size and shape, with a tendency to be longer than wide, as seen in cross section, the long axis being in the direction of the circumference.

The thin-walled parenchyma is not so abundant as in the forms previously described. The cells vary greatly in size. Those which make up the ring of large cells may be as much as 45.5 by 70 microns. No bast fibers are to be found between the phloëm and the parenchyma.

The medullary rays are one cell thick, averaging 3 to 4 in 175 microns at the circumference of the xylem. The cells of the rays are longer in their radial diameter. (Pl. XXIV, Fig. 9).

The xylem is not so compact as in other forms, owing to the greater abundance of tracheal tubes and fewer wood fibers. This condition may be due entirely to habitat conditions, however, altho it is marked in all stems studied.

The pith cavity in the one-year stem is diamond-shaped, the corners less rounded than in *europaeus*. The points alternate with the corners of the stem. The stem itself is flattened on two sides and rounded on the other two (Pl.

XXIII, Fig. 4), a condition different from all other species studied. In the two-year stem the pith cavity is almost square. The pith cells are variable in size, with larger cavities and thicker walls toward the inside. Most of them have comparatively thick walls and are filled with starch grains. The cells containing clustered crystals have thin walls.

## *E. patens* Rehd.

The epidermal cells are flattened, measuring 14.3 microns in their radial diameter by 26.2 microns in their tangential diameter. The outer wall, which averages 10.5 microns in thickness, is not so prominently arched as in other species. Stomata are very numerous (Pl. XXII, Fig. 5).

The outer collenchyma cylinder is strongly developed. At short intervals in the inner margin of this cylinder are large round thick-walled cells like the collenchyma cells which extend into the cylinder of the assimilatory tissue. The cells of the assimilatory tissue radiate more or less around these cells where they are present (Pl. XIII, Fig. 14).

The cells of the assimilatory tissue differ from all previously described in that their long axis as seen in cross section is in the direction of the radius.

There is no connection of collenchyma cells between the outer and inner cylinders. The inner cylinder of collenchyma cells is quite prominent, extending entirely to the phloëm in many places. In other regions thin-walled parenchyma lies between this and the phloëm. The thin-walled parenchyma cells vary in size from 24 by 52 microns to 45 by 70 microns, although the great majority are small. There is not a continuous ring of large cells.

The medullary rays are seven in 175 microns. The cells in some places are quite noticeable because of their large size, some of them being as wide in their transverse diameter as the medium-sized tracheal tubes. Their long axis is in the vertical direction (Pl. XXIV, Fig. 10). Many of them measure as much as five times as long as wide. They are seldom pitted on their horizontal walls. The rays are for the most part one cell thick, but some are two and three cells in thickness.

The pith cells are of moderate but fairly uniform size. Their walls are thick and not easily torn. In the two-year-old stem the cells are living and contain starch. Numerous large cluster crystals are present. The pith cavity is much larger than in any other species studied and is almost circular in cross section in both one- and two-year-old stems, contrasting with the diamond-shaped cavity of most species (Pl. XXIII, Fig. 5).

## *E. americanus* L.

The cells of the epidermis are flattened, irregular in shape and size and are more or less crushed. They average 16.1 microns in the radial diameter by 22.7 in the tangential diameter. The outer wall of the epidermis is thick, measuring 17.5 microns.

The collenchyma cylinder immediately beneath the epidermis is usually only one cell layer in thickness, although it is two cells thick in places. The cells are rather irregular in size and shape.

The inner cylinder, if present, cannot be distinguished from the parenchyma

cells beneath it. The walls of all of these cells are much thicker than the assimilatory tissue cells. There are no collenchymatic connections with the outer collenchyma cylinder.

Cords of bast fibers at the corners of the stem are always present (Pl. XXII, Fig. 6), but these differ from all other species in that they are inside of the cylinder of assimilatory tissue and remain in the cortex, *i. e.*, they are not cut out by cork-forming cells as in other species. The first cork formed is along the four corners and may appear there as early as the fifth or sixth node of the one-year-old stem (Pl. XXIII, Fig. 6). The cork is derived from the cells of the outer cylinder of collenchyma (Pl. XXIV, Fig. 1).

The cells of the assimilatory tissue are thin-walled and have their long axis in the radial diameter. They are much longer than wide in cross section, and as a result this tissue has all the appearance of the palisade tissue of a leaf.

The parenchyma tissue next inside of the assimilatory tissue, as already mentioned, cannot be divided into collenchyma and thin-walled parenchyma cells. All of the cell walls are considerably thicker than those of the assimilatory tissue. The long axes of the cells are in the direction of the circumference. The ring of large cells near the inner margin of this layer is very prominent. These cells measure as much as 52.5 microns in tangential diameter by 35 microns in their radial diameter, while in longitudinal sections some were found measuring 46.5 microns long. Since these cells show no contents, it is presumed their function is that of water storage.

The smaller parenchymalike cells between these large cells and the phloëm, already referred to in other species, are quite prominent in *americanus*. They are short, bluntended tubes measuring about 10.5 microns in their radial and tangential diameters by 63 to 70 microns long.

Most of the phloëm cells look very much alike in cross section, being rectangular in shape. Occasional rows of thinner-walled parenchyma cells at right angles to the medullary rays mark off more or less square areas of the rectangular cells. In longitudinal sections the cells are found to be sieve tubes and tube-like parenchyma cells many of them measuring ½ to 1 mm. in length, and contain simple pits in their walls. Many of these contain the brown secretion which is presumed to be the caoutchouc discussed by Möeller (loc. cit.).

The medullary rays are a single cell in thickness, five or six in 175 microns at the outer margin of the xylem. The long axis of the cells is in the vertical direction. They measure two to three times as long as wide (Pl. XXIV, Fig. 11).

The pith is heterogeneous, being composed of both living and dead cells, the latter having thin walls. There is great variability in the size of the cells. Cluster crystals are numerous; also cells containing caoutchouc are not infrequent. In the one-year stem the pith cavity is diamond-shaped, the corners alternating with the corners of the stem. The region of the vascular bundle is narrow as compared with the cortex or with the pith region. The one-year stem of *americanus* differs from all others studied in that its shape is nearly square in cross section (Pl. XXIII, Fig. 6).

## *E. europaeus nanus* Lodd.

The outer wall of the epidermis in *europaeus nanus* is thick, 12 to 14 microns, and resembles that of *americanus* when seen in cross section. The epidermal cells are somewhat irregular, but are mostly rectangular in shape, measuring 22.75 microns in their tangential diameter by 18.2 microns in their radial diameter. Cells are frequently found which have recently divided. Sometimes this division is in the radial diameter, sometimes in the tangential. The walls of the cells cut off by the tangential division thicken and the cells become collenchymatic. When cork is produced it is in the form of longitudinal flecks scattered promiscuously over the stem. It is epidermal in origin (Pl. XXIV, Fig. 2).

The outer cylinder of collenchyma is one cell thick excepting where it has been added to by the epidermis.

The assimilatory tissue is three to four cells thick and is not cut through by collenchyma cells. The cells are more or less rounded (Pl. XXII, Fig. 7).

The walls of the collenchyma cells of the inner cylinder are not thickened in the angles between cells, but the walls are quite thick. They have simple pits. The cylinder is not of uniform thickness, being much thicker at the angles of the stem; in fact, it seems to be the inceased number of these cells that produces the angles. It is of interest here to note that the stem of *europaeus nanus* has six angles instead of four as in other species (Pl. XXIII, Fig. 7). The first cork forms in flecks between the angles.

Inside of the inner collenchyma layer is a cylinder, for the most part only one cell thick, of thin-walled parenchyma cells. These cells are of about the same size as the inner collenchyma cells. Interspersed with these thin-walled parenchyma cells, or more correctly, just inside of the single-cell layer but interrupted by other large thin-walled cells are patches of cells, as seen in cross section, which have their walls considerably thickened and pitted (Pl. XXIV, Fig. 3). In longitudinal sections these are short tubelike cells. Their walls are not lignified and yet they do not give the same color reactions for cellulose as the phloëm and other prenchyma cells. Similar cells have been discribed for other species; in *europaeus nanus,* however, they are much more strongly developed. No bast fibers are to be found in the cortex of the two-year-old stem of the *europaeus nanus.*

The medullary rays average nine in the arc of 175 microns at the edge of the xylem. They are a single cell in thickness (Pl. XXIV, Fig. 13). The cells have their long axes in a vertical direction but are seldom more than twice as long as wide. The walls are exceptionally thin and sparsely pitted (Pl. XXIV, Fig. 12).

The pith cavity is irregularly circular in outline. The pith cells, which are rather loosely arranged, have fairly thick walls and many of them contain starch. Clustered crystals of calcium oxalate are very frequently found.

## *E. radicans* Sieb.

The outer wall of the epidermis is thin, measuring between 6 and 7 microns. The epidermal cells are of two types. The majority are flattened rectangular cells measuring 10.5 microns in their radial diameter by 21.8 microns in their tangential diameter. Interrupting these at short intervals are larger cells, 24

microns in radial diameter by 21 microns in the tangential diameter. This gives a series of peaks to the outline of the epidermis as seen in cross section (Pl. XXIII, Fig. 8).

The outer collenchyma cylinder likewise consists of larger and smaller cells with pits communicating between them. This layer is typically one cell thick.

The assimilatory tissue is three to five cells in thickness. On one side of the stem the cells of the outer layer of this tissue are elongated in their radial diameter, while the cells of the other layers are round (Pl. XXII, Fig. 8).

On the opposite side of the stem there is a lesser development of this tissue, and all of the cells are round. This is probably due to the fact that the vines from which the specimens were taken were flat on the ground. On the under side of the stem most of the cells are of more or less irregular size and shape.

The inner collenchyma cylinder is well developed but only two to four cells in thickness. The cells are pitted.

The thin-walled parenchyma layer next inside of this inner collenchyma cylinder consists of cells having exceptionally thin walls. They are irregular in size and shape, and it is very seldom that a section is cut without tearing and crushing this layer. There is a considerable development of the thicker-walled, pitted, tubelike cells in patches just outside of the phloëm, especially on the upper side of the stem.

The medullary ray cells are exceptionally large as compared with the other species studied, some of them measuring as much as 14 microns in transverse diameter and occasionally as much as 28 microns in radial diameter. Most of them, however, are roughly almost square as seen in cross section of the stem. In longitudinal sections some are square. The great majority, however, are from 70 to 80 microns in length (Pl. XXIV, Fig 14). They are finely pitted on all surfaces. The rays are one cell in thickness for the most part although occasional rays two cells thick are found.

The pith is homogeneous. The cells are of fairly uniform size and have moderately thick walls. They contain stored starch and a few compound crystals are present.

## *E. alatus* Reg.

The outer wall of the epidermis in a section of the two-year stem measures 19.75 microns in thickness. The epidermal cells are sharply pointed outward, but from the margin of the outer wall the sides are perpendicular to the base. The epidermis is one to two cells thick. The cells measure 18.5 microns in the radial diameter by 12.25 microns in the tangential diameter (Pl. XXII, Fig. 9).

The outer collenchyma cylinder is strongly developed, being three to four cell layers in thickness. Beneath the cork wings these cells are stretched so much that it is impossible to distinguish them from other types of cells. The cork wing takes its origin from the epidermal cells (Pl. XXIV, Fig. 4). The shrubs from which specimens for these studies were taken were growing slowly, which may account for the precocious development of the wing somewhat at variance with descriptions of other writers. Plate XXIII, figure 9, is from a section cut two millimeters from the base of the terminal bud. The wings were well developed on three sides and just starting on the fourth; but two

millimeters further back this wing was as large as the other three. The other tissues of the stem were equally well developed in this section.

The cork cells of the cork wings are quite large, thin-walled and elongated radially (Pl. XXIV, Fig. 5). Plate XXIV, figure 4, shows only a few of the cork cells at the corner of the wing, where they are very small.

The chlorophyll-containing layer is two to three cells in thickness and is not cut through by the collenchyma tissue, although beneath the wings these cells, along with all others, become so stretched that they cannot be distinguished from the collenchyma cells. The cells of the assimilatory tissue are small, roughly rectangular in shape, with their long axes in the radial diameter.

The inner collenchyma cylinder is well developed. The cells vary greatly in size, from 5 microns to 63 microns in the tangential diameter, which is the long axis of the cell. The larger cells are at the inner circumference of the cylinder and only rarely is one found which is as large as the measurement given. Great numbers of large clustered crystals are stored in the cells of this cylinder.

The parenchyma cells inside of the inner cylinder of collenchyma is composed for the most part of large cells. The cell walls are exceedingly thin and easily torn.

The medullary rays are one cell in thickness and average four to the arc of 175 microns at the edge of the xylem (Pl. XXIV, Fig. 15).

The pith is heterogeneous. The cells have thick walls, but vary greatly in size. They are empty excepting for an occasional compound crystal. The pith cavity is diamond-shaped and is smaller than in the other species studied. The points of the diamond are opposite the four wings. Using the position of the pith cavity as found in the other species as a criterion, it would seem that in *alatus* the wings form between the lines which produce the angles on the other species of the genus.

## SUMMARY OF THE ANATOMY OF THE TWO-YEAR-OLD STEM.

The stems of the shrubs and vines of the genus *Euonymus* are often said to be characteristically four-angled. This statement is true in a general way, the angles being produced by the excessive development of collenchyma tissue under the epidermis. In some species this condition is so weakly developed that it is almost impossible to locate the angles. The condition has its typical development in *E. europaeus, atropurpureus, bungeanus* and *maackii.* An extreme condition is found in *americanus,* where the young stems are almost square. In *europaeus nanus* the young stems are distinctly six-sided. In *alatus* the angled characteristic of the others do not appear, but large cork wings are present between the lines where the angles are formed on the other species. In *patens* and *radicans* the angles are not apparent.

The outer epidermal wall throughout the species investigated is relatively thick. In *europaeus, bungeanus, patens, europaeus nanus* and *radicans* it is as thick or thicker than half the radial diameter

of the epidermal cells, and in *americanus* and *alatus* it is thicker than the cavities in their radial diameter. In only two species studied, *atropurpureus* and *maackii,* it is less than half of the radial diameter of the cavities of the epidermal cells.

In *atropurpureus* and *alatus* the epidermal cells are pointed on the outer side and are longer in the radial than in the tangential diameter. In *alatus* the epidermis is variable, from one to two cells thick. In *maackii* the two diameters are of about equal length and the cells are somewhat pointed. In the remaining species the tangential diameter is the longest, *europaeus* and *patens* varying from one to two cells in thickness. The outer cell surface is rounded in *europeaus, bungeanus* and *patens,* but almost flat in *americanus, radicans* and *europaeus nanus.* In *radicans* single cells much larger than the others occur at short intervals, producing small peaks over the epidermis.

Cork is relatively slow in forming in most species. The cork wings of *alatus* are very precocious in their development. In *atropurpureus, europaeus, bungeanus* and *americanus* lines of cork appear along the angles of the stem usually by the early part of the second year of growth. In the two first-named species these lines take the form of rather temporary, weakly developed wings. In *bungeanus* these winglike growths appear occasionally, very weakly developed. The spaces between these lines remain more or less green from two to five years. In all species examined the cork, excepting in the wings of *alatus* and in that formed at the angles of the stem in the above-mentioned species, arises as little brown longitudinal flecks which resemble lenticels in appearance. These multiply in number and size until the stem is covered.

From my own findings and the work of other investigators it may be said that the cork usually is of epidermal origin. At the angles of the stem in *atropurpureus* and *americanus* however, it is derived from the collenchyma tissue beneath the epidermis.

Next beneath the epidermis is a layer of colorless collenchyma cells. This layer is only one cell thick in *patens, americanus, europaeus nanus* and *radicans,* but more than one cell thick in *atropurpureus, europaeus, bungeanus, maackii* and *alatus.* In *patens* and *radicans* large, round, thick-walled colorless cells occur in (*radicans*) or just beneath (*patens*) this layer of tissue.

A second layer of collenchyma tissue inside of a layer of chlorophyll-containing cells is characteristic of the genus, altho this is variable in the degree of its development. In some cases it grades

off into an inner layer of thin-walled parenchyma cells so gradually that it is difficult to ascertain the dividing line.

The two cylinders of collenchyma tissue are connected with each other by collenchyma cells at the four corners of the stem in *atropurpureus, europaeus, bungeanus* and *maackii,* but not in the other species. These collenchyma cells cut through the layer of chlorophyll-containing cells and thus produce the white lines which show through the epidermis in young stems.

The chlorophyll-containing layer is usually from three to five cells in thickness. In *atropurpureus* and *europaeus nanus* the cells are almost isodiametric in shape; in *europaeus, bungeanus* and *maackii* they have their long axes in a tangential direction, while in *patens, americanus, radicans* and *alatus* the long axis is in the radial diameter. In these last-named species this layer frequently looks very much like the palisade layer of leaves. The degree of development in this direction seems to be in response to the sunlight, since in *radicans* these assimilatory cells on the side of the stem which lies on the ground are irregular to isodiameteric in shape.

Inside of the inner collenchyma cylinder is a layer of parenchyma tissue of varying thickness. The cell walls of this tissue are characteristically thin, but in some of the species they are rather thick. In those forms in which the walls are thickened they are rather conspicuously pitted. The cells of this layer always have their long axis in the tangential direction. They vary in size, being smaller in the outer circumference and gradually becoming larger towards the inner circumference. These large cells at the inner circumference reach their greater development in *americanus.*

Between this layer and the phloëm are irregular patches of smaller blunt-ended tubelike cells. In most species the walls of the cells are only slightly thicker than those of the surrounding parenchyma cells, but in others, especially *europaeus nanus,* the walls become greatly thickened.

Bast fibers are not formed in the cortex of *maackii, patens, europaeus nanus, radicans* or *alatus.* In *atropurpureus* rather large bundles of fibers are found at the corners of the stem in the tissue just beneath the outer collenchyma cylinder. Also scattered fibers, single or in groups of two or three, are found just outside of the phloëm. In *europaeus* scattered fibers are found outside of the phloëm and small bundles may or may not develop at the corners of the stem. In *americanus* bundles of fibers develop at the corners

of the stem, but in this species they are inside instead of outside of the assimilatory tissue.

The vascular bundles of the stem were quite similar in all species studied. The cells of the phloëm region are all thin-walled and more or less rectangular in shape, so that it is impossible to distinguish the sieve tubes and companion cells in cross sections. In the xylem wood parenchyma is scarce and tracheids with bordered pits are only infrequently found. The tracheal tubes are broadly pitted and have spiral or concentric thickenings of the walls. The wood fibers are mostly pitted and assist in the transportation of water.

The medullary rays in all species are normally one cell wide, although rarely here and there a ray of two cells in thickness was observed. In *maackii, patens, americanus, europaeus nanus* and *radicans* the cells of the medullary rays vary from square to long, the long axis being in the vertical direction. In *radicans* some of these cells are extremely long. They are very thin-walled and finely pitted. In *europaeus nanus* the cells are small, thin-walled and finely pitted. The rays in this species are seldom more than three to four cells high and never more than one cell wide. In *atropurpureus* the rays are prominent. The cells vary from square to long, but some of the long cells have their long axes in the vertical direction while others have it in the radial direction. In *europaeus, bungeanus* and *alatus* most of the cells are oblong and all have their long axes in the radial direction. Starch is stored in the medullary rays of all species investigated.

The pith throughout the group is alike in that the cells are longer in their vertical diameter, and compound crystals of calcium oxalate are found in all species. Starch is not stored in the pith of *atropurpureus, europaeus* and *alatus,* but is found in varying quantities in the other species. The cells are of different sizes in *atropurpureus, europaeus, bungeanus, maackii, americanus* and *alatus,* but more or less uniform in size in *patens, europaeus nanus* and *radicans.* According to the types of pith as described by Gris (*5*), the species studied are grouped as follows:

Homogeneous—*patens, europaeus nanus* and *radicans.*

Heterogeneous—*bungeanus, americanus* and *maackii.*

Empty—*atropurpureus, europaeus* and *alatus.*

## THE PETIOLE.

### *E. atropurpureus* Jacq.

(Pl. XXVII, Fig. 1.)

The petiole is strongly arched out on the upper surface between prominently projecting margins.

Two types of vascular bundles are present: The large central bundle is very curved with the ends bent sharply in. Opposite each upper outer angle where the ends bend in on each side is a small closed vascular bundle with the phloëm completely surrounding the xylem.

Outside of the vascular bundles the walls of all the cells are a little thickened and are finely pitted. Finely pitted collenchyma tissue occupies a layer five cells thick around the outside margin, immediately around the phloëm and inside of the xylem. One or two small vascular bundles occur at the bases of the projecting margins.

Compound crystals are abundant in the phloëm and are scattered in the outer parenchyma and collenchyma.

### *E. europaeus* Linn.

(Pl. XXVII, Fig. 2.)

The petiole is somewhat arched outward on the upper surface between slightly projecting margins.

The vascular bundle it strongly curved with the ends curved in. Opposite each of the upper outside angles of this central bundle is a small open bundle.

Just beneath the epidermis is a layer five to six cells thick of strongly developed, unpitted collenchyma cells. Another layer of smaller collenchyma cells is just outside of the phloëm, but not inside of the xylem. Comparatively large, more or less rounded, thin-walled parenchyma cells extend between these two layers on the under and lateral sides and between the xylem and outer collenchyma on the upper side.

Compound crystals are abundant in the phloëm and thin-walled parenchyma and are found here and there in the collenchyma.

### *E. bungeanus* Maxim.

(Pl. XXVII, Fig. 3.)

The upper surface is strongly arched inward from slightly projecting margins. The large vascular bundle is a wide, open arc, not bent in at the ends. A small open bundle is opposite each end of the arc.

Just beneath the epidermis is a layer four to five cells thick of greatly thickened collenchyma cells. Their cavities are angular and each cell connects with neighboring cells by a single pit to each cell. There is no collenchyma layer immediately outside of the phloëm.

The parenchyma tissue is composed of fairly thick-walled, finely pitted cells on the outer margin, small thin-walled cells just outside of the phloëm and inside of the xylem and large thin-walled cells between these two layers.

Compound crystals are scattered in the phloëm and parenchyma.

## *E. maackii* Rupr.

(Pl. XXVII, Fig. 4.)

In cross section the petiole of *maackii* is longer than wide. The upper surface is slightly curved outward between projecting margins.

The vascular bundle is curved and slightly bent in at the ends. No small bundles are present at the angles of the one large bundle.

The collenchyma layer beneath the epidermis is strongly developed and is three to four cells in thickness. The cells are finely pitted. The tissue immediately outside of the phloëm is variable. Small patches of the cells have their walls so thickened as to almost obliterate the cavity of the cells. Others are hardly thickened enough to be called collenchyma.

The parenchyma cells have only slightly thickened, unpitted walls excepting those below the phloëm, which are quite large and thin-walled. Crystals are in the phloëm and parenchyma, but not abundant.

## *E. patens* Rehd.

(Pl. XXVII, Fig. 5.)

The petiole is wider than long in cross section. There are no projecting margins. The upper surface is not smooth, due to small, protruding irregularities on the surface. In general outline it is curved inward for about the middle third; the outer third on each side curves outward.

The vascular bundle is flattened, curved at the ends, but not bent in.

The collenchyma layer beneath the epidermis is prominently pitted and is three to four cells thick. The cells have very thick walls and are considerably smaller on the upper than on the lower side of the petiole. That outside of the phloëm is irregularly developed and is not in a continuous layer. It is composed of small cells.

The parenchyma cells between the collenchyma layers have thick walls, are very noticeably pitted and have abundant large intercellular spaces between them.

Compound crystals are found in the phloëm and some in the collenchyma, but are most abundant in the outer region of the parenchyma.

## *E. americanus* L.

(Pl. XXVII, Fig. 6.)

The upper surface curves inward. Small, blunt, single-cell trichomes are present on all sides of the petiole.

The vascular bundle is an open arc not curved in at the ends.

The collenchyma layer on the upper side and around the corners of the petiole is very strongly developed and is pitted. It merges into a thick-walled parenchyma layer which extends to the level of the tips of the vascular bundle. Beneath this and inside of the arc of the xylem the parenchyma cells are rounded and thinner-walled. Around the remainder of the circumference of the petiole the collenchyma is difficult to distinguish from the parenchyma, in so far as thickness of cell walls is concerned. The cells have their long axes in the direction of the circumference and any intercellular spaces are

inconspicuous. The collenchyma layer outside the phloëm is poorly developed. There are scattered groups of small collenchyma cells. The parenchyma cells have very thick walls, very conspicuously pitted and large, prominent intercellular spaces. There are very few crystals.

## *E. europaeus nanus* Lodd.

(Pl. XXVII, Figs. 7 and 8.)

This petiole is very small. Figure 7 is photographed at the same magnification as the others on the plate. The upper surface is flat.

The vascular bundle is in the form of a thick arc, almost fan-shaped.

The collenchyma tissue is not strongly developed. Around the margin of the petiole it is one to two cells in thickness. The cells are more or less rectangular in shape. On the upper surface the lateral cell walls are not thickened. This causes a layered appearance in this region. The cells are pitted.

Immediately outside of the phloëm and inside of the xylem the cells are small and have only slightly thicker walls than the thin-walled parenchyma which surrounds them. The walls of the parenchyma cells gradually get thicker toward the outer margin of the petiole until they merge into the collenchyma layer. Crystals are very few.

## *E. radicans* Sieb.

(Pl. XXVII, Fig. 9.)

The outline of the cross section of the petiole of *radicans* is irregular, due to projections produced by occasional extremely large epidermal cells, or at times also to an enlarged collenchyma cell which shoves the epidermal cells out. As noted in the description of the stem of this species, the epidermal cells and the collenchyma cells are each quite uniform in size and shape excepting at short intervals, where much larger cells occur.

The upper surface of the petiole curves inward from rounded corners.

The vascular bundle is a broadly opened arc.

Groups of very small cells are immediately outside of the phloëm, but in this species they are not collenchymatous.

The collenchyma beneath the epidermis is one to two cells thick. The cell walls are pitted. The cavities of these cells are more or less rounded The parenchyma cells are rounded, have heavy, inconspicuously pitted walls and prominent intercellular spaces.

Crystals are few and scattered, with none in the phloëm.

## *E. alatus* Reg.

(Pl. XXVII, Fig. 10.)

Occasional short single-cell trichomes are present. The upper surface is arched out in a peak almost to the level of the tips of the projecting margins. The vascular bundle is fan-shaped and not concave inside of the xylem.

There is no parenchyma layer, the entire region from phloëm to epidermis being a highly developed collenchyma. Even the phloëm parenchyma cells

have their walls greatly thickened. At the corners inside of the marginal projections the cells are rather loosely arranged with large intercellular spaces. Crystals are numerous.

### SUMMARY OF THE ANATOMY OF THE PETIOLE.

There are some very noticeable differences in the general outline of the cross section of the petioles among the species studied.

Scattered trichomes were found on the upper surface in *alatus* and on all surfaces in *americanus*. In *patens* the upper surface has many small irregularities in its contour. In *radicans* smaller irregularities occur more or less at intervals all around the petiole. In this case, as was described in the stem for this species, the epidermis has much larger cells at intervals, which produce small, peaked elevations.

The margins project up above the top in *atropurpureus, europaeus, bungeanus, maackii,* and *alatus,* but not in *patens, americanus, radicans,* and *europaeus nanus.*

The upper surface is flat in *europaeus nanus.* It is convex in *atropurpureus, europaeus, maackii* and *alatus,* and concave in *bungeanus, patens, americanus* and *radicans.* In *patens* the corners round in so gradually that only the middle third is concave.

The vascular bundle is more or less in the form of an arc in all species excepting *alatus,* where it is fan-shaped. In *patens* the arc is greatly flattened with only the ends cuurved. In *atropurpureus, europaeus* and *maackii* the ends of the arc are bent in sharply. Small bundles are present just above and outside the ends of the arc in *atropurpureus, europaeus* and *bungeanus.* In *atropurpureus* these small bundles are completely surrounded by phloëm, and there are also other small bundles at the bases of the marginal projections.

Bast fibers were not found in the petioles of any of the species studied.

The distribution of collenchyma tissue is somewhat variable in the nine species. In *alatus* all cells outside of the vascular bundle are strongly collenchymatous, while in *radicans* the only collenchyma tissue is a layer one to two cells thick around the outer margin, and even this is not strongly developed collenchyma. In *alatus* these cells are not pitted, but in *radicans* they are. In the other species, *atropurpureus, europaeus, bungeanus, maackii, patens, americanus* and *europaeus nanus,* there is a definite layer of collenchyma cells around the outer margin next beneath the epidermis. In *americanus*

this layer is only two or three cells thick around the lower side, but is four to five rows thick across the upper surface. In *europaeus nanus* it is only one cell thick around the lower side, and these cells do not have greatly thickened walls. On the upper surface it is four to five rows thick, but here the side walls are not thickened, while the upper and lower walls are thick. These collenchymatic cells were not pitted in *europaeus* and *alatus*. In *atropurpureus* and *maackii*, the pits were very fine, while in *bungeanus, patens, americanus, radicans* and *europaeus nanus* the pits were quite prominent.

Just outside of the phloëm there was a layer of small collenchyma cells in *atropurpureus, maackii, patens* and *americanus* and, of course, *alatus*. In *europaeus, bungeanus, radicans* and *europaeus nanus* very small thin-walled parenchyma cells occupied this region.

Similar small collenchyma cells were found just above the xylem in *atropurpureus* and *bungeanus* but in all other species these cells were very small, thin-walled parenchyma.

The region between the vascular bundle and the outer collenchyma is occupied by rounded parenchyma cells. These parenchyma cells are thin-walled and without pits in *europaeus, maackii* and *europaeus nanus;* thin-walled with very fine pits in *atropurpureus* and *bungaeus;* while they have rather thick pitted walls in *patens, americanus* and *radicans*.

## THE LEAF BLADE.

### *E. atropurpureus* Jacq.

In surface view the epidermal cells of the upper surface of the leaf are irregular but have almost straight boundaries. The palisade cells are rather loosely arranged so that small intercellular spaces often reach the epidermis (Pl. XXV, Fig. 1). The cells of the lower epidermis are somewhat sinuous and are smaller (Pl. XXV, Fig. 2). The side walls of some of the cells of the upper epidermis are finely pitted, those of the lower epidermis are not pitted.

In cross section the cells of the upper epidermis are taller than those of the lower, in both they are more or less rounded and in both the cells are slightly broader than high. The outer walls on both surfaces curve outward; those of the upper epidermis are slightly thicker than those of the lower. The side walls are thinner than the outer walls and the inner walls are still thinner than these (Pl. XXVI, Fig. 1).

Stomata are present on the lower surface only. They are broadly elliptical in outline and are almost level with the surface. Short, blunt, single-cell trichomes are present on the lower surface of the leaf.

The palisade layer is two-rowed. The cells of the upper row are from three to four times as high as wide; those of the lower row are somewhat shorter.

The spongy mesophyll is from four to five cells thick, the cells are rounded or slightly elongated parallel to the surface. The walls of all mesophyll cells are very thin.

The vascular bundle of the midrib is only slightly curved. The bundle is surrounded by thin-walled parenchyma (Pl. XXIV, Fig. 16). A layer one to two cells thick above the xylem contains chloroplasts and is continuous with the palisade of the leaf. Collenchyma cells fill the region from the parenchyma to the epidermis on both the upper and the lower surfaces. The larger veins connect with both upper and lower surfaces of the leaf by rather large collenchyma cells. The smaller veins are completely immersed.

Compound crystals are found in the cells of all tissues of the leaf, but not abundantly in any. They are more numerous in the phloëm of the midrib and in the parenchyma sheath of the smaller veins.

## *E. europaeus* Linn.

The cells of the upper epidermis are irregular in size and shape, but for the most part have almost straight walls (Pl. XXV, Fig. 3). The cells of the lower epidermis are quite variable in size, but most of them are much smaller than those of the upper epidermis. They are slightly sinuous (Pl. XXV, Fig. 4). The side walls of the upper epidermis are finely pitted; those of the lower are not. The palisade cells are quite compactly arranged. Stomata are found only on the lower surface. They are broadly elliptical and protrude but slightly below the level of the epidermal cells. No trichomes are present.

In cross section the cells of the upper and lower epidermis are about the same height. The outer walls of both are arched out slightly; those of the upper epidermis are much thicker than those of the lower. The side walls of both of the upper and the lower epidermis are quite sinuous and are only a little thicker than the curved inner wall.

The palisade layer is two rowed. The cells of the upper row are about four times as tall as broad. Those of the lower row are very irregular in shape and size and are not more than one and a half to two times as tall as broad. Most of them are broader than those of the upper layer.

The spongy mesophyll is three to four cells thick. The cells are rounded or irregular in shape and more or less compact (Pl. XXVI, Fig. 2).

The midrib protrudes on both sides (Pl. XXIV, Fig. 17). It, as well as the larger veins, are connected with both surfaces of the leaf by collenchyma tissue. The vascular bundle is a broadly open arc not bent in at the ends. Above, collenchyma tissue forms the ridge which protrudes on the upper surface of the leaf. Rounded cells containing chloroplasts extend in at least a third of the width of the rib on each side just beneath the collenchyma tissue. Between these cells and the xylem are comparatively large thin-walled parenchyma cells. Beneath the bundle outside of the phloëm, first small then larger thick-walled somewhat collenchymatous cells make up the portion of the rib which protrudes beneath the leaf. A layer four to six cells wide of collenchyma is around the margin. No other sclerenchyma cells are present. The larger veins extend through, both above and below, by strongly developed

collenchyma cells. The smaller veins are completely immersed and surrounded by a parenchyma sheath.

Occasional compound crystals are found in the upper epidermis as well as in the upper palisade and the spongy mesophyll, but they are by far more numerous in the lower row of the palisade layer of the leaf.

## *E. bungeanus* Maxim.

In surface view the cells of the upper epidermis are fairly regular is size with straight sides. The palisade cells are compactly arranged (Pl. XXV, Fig. 5). On the lower epidermis the cells are only slightly smaller than those of the upper and are not so regular in size or shape; the sides are frequently more or less curved, but are not sinuous (Pl. XXV, Fig. 6). The side walls of both the upper and the lower epidermis are finely pitted. Stomata are present on the lower surface only. They are rather broadly elliptical in shape.

In cross section the side walls of both the upper and the lower epidermises are not straight; some are curved, some are quite sinuous, some slant one direction and some the other. The outer cell walls curve outward slightly and are only a little thicker than the side walls. The cells on both surfaces are broader than tall (Pl. XXVI, Fig. 3).

The palisade tissue is two-rowed. The cells of the upper row are more than three times as tall as broad, those of the lower row are broader and are less than three times as tall as broad.

The spongy mesophyll is for the most part rather compact. It is composed of rounded, somewhat flattened cells. All of the mesophyll cells have very thin walls.

The midrib protrudes both above and below the leaf (Pl. XXIV, Fig. 18). The vascular bundle of the midrib is a very greatly flattened arc. It is surrounded by parenchyma cells which extend out to a collenchyma layer three to five cells thick on both the upper and lower surfaces. No sclerenchyma fibers are present in the midrib. Chlorophyll-containing tissue does not extend entirely across the upper surface of the vein. The lateral veins are immersed above, but extend through on the under side by slightly thickened parenchymalike cells.

A few compound crystals are scattered here and there in the tissues of the leaf and are not more abundant in one tissue than another.

## *E. maackii* Rupr.

In surface view the cells of both epidermises are elongated, mostly twice as long as broad, with slightly curved edges. The elongation does not seem to bear any relationship to the long axis of the leaf (Pl. XXV, Figs. 7 and 8). The side walls of the cells of the upper epidermis are finely pitted; those of the lower are not. The palisade cells are rather loosely arranged. The cells of the lower epidermis are smaller than those of the upper, and are somewhat sinuous in outline. The cells of the spongy mesophyll, as seen through the epidermal cells, are smaller than the cells of the epidermis and are mostly rounded or elongated. The stomata are rather elongate-elliptical in shape and are found only on the lower surface.

In cross section (Pl. XXVI, Fig. 4) the cells of both epidermises are broader

than tall. The outer walls curve outward. The outer walls of the upper epidermis are thicker than those of the lower and both are thicker than the side or inner walls. The side walls of the cells of both the upper and lower epidermises vary from straight to sinuous.

The palisade tissue is two rows high. The cells of the upper row are usually more than three times as high as wide. The cells of the second row are more than twice as high as broad. About two-thirds of the thickness of the leaf is occupied by palisade tissue. The spongy mesophyll is composed of loosely arranged, rounded cells, three to four cell layers thick.

The midrib protrudes on both upper and lower surfaces (Pl. XXIV, Fig. 19). The vascular bundle is a broad arc and is surrounded by a broad region of thin-walled parenchyma tissue. No sclerenchyma fibers accompany the bundle. Rounded chlorophyll-containing cells extend entirely across the upper surface of the rib. Above, outside of the assimilatory tissue, collenchyma tissue extends to the epidermis. On the lower side a layer of collenchyma tissue, five to six cells thick, is beneath the epidermis. The lateral veins extend through to both surfaces by rather large collenchymatous cells.

Compound crystals are scattered in all tissues, but are most numerous in the lower palisade layer, where they are contained in large rounded cells.

## *E. patens* Rehd.

In surface view the cells of both surfaces are about the same size (Pl. XXV, Figs. 9 and 10). The cells of the upper epidermis are less than half as large as the corresponding cells of *maackii*. Their margins are slightly rounded and their side walls are pitted. The palisade tissue is fairly compact. The margins of the cells of the lower epidermis are irregular, usually curved but not sinuous. The side walls are pitted. The cells of the spongy mesophyll are rounded and irregular in shape with protruding processes. They are larger than the cells of the lower epidermis.

Stomata are present on the lower surface only. They are rather elongate elliptical in shape and protrude only silghtly below the surface (Pl. XXV, Fig. 11).

In cross section the cells of both surfaces are broader than tall. In the upper epidermis the outer cell walls are almost flat and are thicker than the outer walls; the inner wall is thicker than the side walls. The side walls are straight for the most part, although many are quite sinuous. In the lower epidermis the outer wall is thicker than the other walls, but is not so thick as the outer wall of the upper epidermal cells. The side walls are quite sinuous.

The palisade layer is mostly three rows in height and occupies about half the thickness of the leaf. The cells of the top row and the second row are about the same size, being a little more than twice as high as wide. Those of the third row are only slightly elongated in the vertical direction (Pl. XXVI, Fig. 5).

The midrib protrudes on both surfaces only slightly (Pl. XXIV, Fig. 20). The vascular bundle is a greatly flattened arc and is surrounded by thin-walled parenchyma. A bundle of bast fibers is just outside of each end of the phloëm Assimilatory tissue extends entirely across the upper surface. Outside of the assimilatory tissue to the epidermis is collenchyma. On the lower surface

collenchyma is confined to a very narrow layer beneath the epidermis. Bast fibers accompany many of the smaller veins on their under side. These smaller veins have a prominent parenchyma sheath. They do not extend through to the surface of the leaf.

Compound crystals are fairly numerous and cannot be said to be more abundant in one tissue than another.

## *E. americanus* L.

In surface view the cells of the upper epidermis are rounded or quite sinuous in outline. At the points where the cells join there is usually a very definite triangle produced by pectic modification of the side walls where three cells join (Pl. XXV, Fig. 12). The side walls are pitted. The palisade cells are quite compact. Short, blunt, single-cell trichomes (Pl. XV, Fig. 14) are found along all the larger veins on the upper surface and rarely on the epidermis other than above the veins.

The cells of the lower epidermis are quite sinuous but join together completely (Pl. XXV, Fig. 13). The side walls are finely pitted. No trichomes are present on the lower surface. The stomata, which are found only on the lower surface, are almost circular in surface view.

In cross section the cells of the epidermises are broader than tall. The outer wall of cells of the upper epidermis protrudes slightly and is somewhat thickened. The side walls are bent or sinuous. The cells of the lower epidermis are not so tall as those of the upper. The outer walls are thin.

The palisade layer is mostly one cell thick. The cells are broad, about twice as tall as wide. The spongy mesophyll occupies about two-thirds of the thickness of the leaf. The cells are short and stretched, with large intercellular spaces (Pl. XXVI, Fig. 6).

The midrib protrudes slightly on both surfaces (Pl. XXIV, Fig. 21). The vascular bundle is almost fan-shaped. Small bundles of bast fibers are scattered in the parenchyma just outside of the phloëm. In some leaves small bundles of very thick-walled sclerenchyma cells were found just above the xylem; in others they were not present. Assimilatory tissue extends entirely across the vein. Collenchyma cells above this tissue produce the elevation on the upper side of the leaf. Below the bundle a layer of greatly thickened collenchyma cells occupy most of the space between the vein and the epidermis.

The smaller veins are immersed on the upper side, but connect with the epidermis by collenchyma cells on the lower. Bast fibers frequently accompany these smaller veins.

Compound crystals are chiefly found in the spongy mesophyll, but are not absent from the other tissues.

## *E. europaeus nanus* Lodd.

In surface view the cells of the upper epidermis are mostly elongate, five- or six-sided polygons with straight sides. There is no correlation between the long axis of the leaf and the long axis of these cells. The side walls are prominently pitted with long oval pits. The palisade cells are quite compact (Pl. XXV, Fig. 15). On the lower epidermis the cells are only slightly smaller than those

of the upper. They are not so regular in shape and in outline the walls are not straight but deeply curved, almost sinuous (Pl. XXV, Fig. 16). The pits in the side walls are like those of the upper epidermis but are finer. Stomata are present on the lower side of the leaf only.. They are elongate-elliptical in shape and have their long axes parallel with the midrib. The spongy mesophyll cells are rather small and rounded with small air spaces between.

In cross section the cells of the upper epidermis are much broader than tall. The outer wall protrudes usually to rather a broad peak, and is quite thick as compared with the previous species described. The side walls are straight and of about the same thickness as the inner wall. The lower epidermal cells are almost square or rectangular in shape. The outer wall is only slightly thicker than the others.

The palisade tissue is mostly three-rowed and occupies a little less than half of the thickness of the leaf. The cells of the upper layer are about twice as tall as broad. Those of the two lower rows are variable in form and are very loosely arranged. The spongy mesophyll in cross section shows up as rather compact, squarish cells (Pl. XXVI, Fig. 7).

The midrib protrudes only very slightly on the upper surface and but little on the lower (Pl. XXIV, Fig. 22). The vascular bundle is a greatly flattened arc. There is no collenchyma tissue in the midrib. Above the vascular bundle an outer row of palisade and below this one to two rows of rounded cells containing chlorophyll reach to the epidermis. Below the bundle almost round, thin-walled parenchyma cells fill all of the space to the epidermis. There are no bast fibers. The lateral veins are all completely immersed.

Compound crystals are found mostly in the spongy mesophyll.

## *E. radicans* Sieb.

In surface view the cells of the upper epidermis are irregular polygons with mostly straight sides (Pl. XXV, Fig. 17). The side walls have prominent round pits. The palisade cells are compactly arranged. The cells of the lower epidermis are smaller and have slightly curved boundaries (Pl. XXV, Fig. 18). The side walls, also, have prominent round pits. Stomata occur on the under surface only and are broadly elliptical in shape.

In cross section the cells of the upper epidermis are broader than tall. The outer walls bulge outward and are only a little thicker than the other walls, all being relatively thick. The side walls are straight and the inner walls are convex, producing an almost oval cavity. The cells of the lower epidermis are smaller, but in general shape they resemble the upper epidermal vells. The outer wall is thicker than the side walls or the inner wall (Pl. XXVI, Fig. 8).

The palisade layer is made up of two rows of cells of about the same size and shape. They are broad and less than twice as tall as broad for the most part; frequently they are almost oval. The layer occupies one-third or less of the thickness of the leaf. The cells of the spongy mesophyll are much larger, irregular in shape and loosely arranged with large air spaces.

The midrib protrudes a little on the upper surface and not at all prominently on the lower (Pl. XXIV, Fig. 23). The vascular bundle here is an open arc and is accompanied outside of the phloëm by bundles of bast fibers.

Assimilatory tissue extends entirely across the upper surface of the vein. Above this are a few collenchyma cells. The lower portion of the vein is composed chiefly of thin-walled parenchyma cells, excepting for a very narrow layer of collenchyma just beneath the epidermis. The larger veins are immersed, but are surrounded by thick-walled cells which extend out to within one or two cells of the epidermis on both surfaces. Bast fibers are not present. Crystals are not abundant, but are scattered through all of the tissues.

## *E. alatus* Reg.

In surface view the cells of the upper epidermis are irregular polygons with rounded borders (Pl. XXV, Fig. 19). The side walls are finely pitted. Scattered trichomes are present on the epidermis above the veins. The palisade cells are compactly arranged. The cells of the lower epidermis are quite sinuous in shape (Pl. XXV, Fig. 20). In some of the cells small pits are present in the side walls, but in the majority they are not present. Stomata occur only on the under surface and are rather elongate-elliptical in shape.

A striking feature found in leaves cleared in chloral hydrate is the lower layer of the spongy mesophyll (Pl. XXV, Fig. 21). This layer contains a substance that becomes somewhat of a salmon color and is almost opaque in this reagent only. The cells are extremely large as compared with all other cells of the leaf and in shape resemble giant flattened amebas, joined together by blunt pseudopods, leaving large air spaces between. The other mesophyll cells can be seen where they project over the air spaces and are of the same shape, but are colorless. This is in great contrast with the description of the spongy mesophyll as given by Metz (*8*), who says that they are "small oval cells." It is probable that he made this statement after observing the cells in cross section only. (See Pl. XXVI, Fig. 9.)

In cross section the cells of the upper epidermis are much broader than tall. The outer walls curve outward and are only slightly thicker than the other walls. The side walls are mostly almost straight; the inner walls curve inward somewhat. The cells of the lower epidermis are irregular in size and shape, as would be expected because of their sinuousness. The outer wall is slightly thicker than the others and is flat in some cells, bulged out in others. The side walls are straight in some cells, bent in others.

The palisade layer is very irregular—one, two or even three cells thick. The two- to three-rowed condition predominates. This layer occupies about half of the thickness of the leaf, and in places single long slender cells reach the entire distance across. Where two or three rows are found the inner rows are irregular in size, shape and position. The walls of almost all of the palisade cells are curved or bent. The cells of the spongy mesophyll appear rounded and fairly small when seen in cross section.

The midrib protrudes sharply on both surfaces (Pl. XXIV, Fig. 24). The vascular bundle is a thick open arc accompanied on the lower side by several bundles of bast fibers, on the upper side by bundles of very thick-walled sclerenchyma cells. The assimilatory tissue extends across the upper surface of the vein, but extends up into the elevated region. Collenchyma cells extend out to the epidermis. Between the assimilatory tissue and the xylem is

parenchyma tissue. Below the bundle the entire vein is composed of thick-walled collenchyma tissue. The lateral veins are connected to both surfaces by large collenchyma cells. Below the vascular bundle of these veins large bundles of bast fibers are present.

Large compound crystals were found in all of the types of cells in the cross section of the leaf. They were most numerous around the veins, where there were often six or seven large crystals. Only occasionally were crystals found in either the upper or lower epidermis, more frequently in the lower, a few in the palisade, and fairly numerous in the spongy mesophyll.

### SUMMARY OF THE ANATOMY OF THE LEAF BLADE.

The cells of the upper epidermis in all of the nine species studied were broader than tall. In surface view all are polygonal in shape, the sides of the polygon being more or less straight in *atropurpureus, europaeus, bungeanus, europaeus nanus* and *radicans,* curved in *maackii, patens* and *alatus,* but quite sinuous in *americanus.* In size the cells of *maackii, americanus* and *europaeus nanus* are quite large, those of *atropurpureus, europaeus, radicans,* and *patens* are intermediate, while those of *bungeanus* and *alatus* are small.

The cells of the lower epidermis are of about the same size as those of the upper in *bungeanus, patens* and *alatus,* but are smaller than the upper in all other species. They are also polygonal, but the sides of the polygon are more or less curved in all the species, even quite sinuous in *alatus* and *americanus.*

The side walls of the cells of the upper epidermis were pitted in all the species studied, and those of the lower epidermis in *bungeanus, patens, americanus, europaeus nanus, radicans* and *alatus.* The pits were very fine in *europaeus, atropurpureus, bungeanus, maakii* and *alatus,* but were quite prominent in the others. In *europaeus nanus* the pits are very long ovals in shape.

Stomata are found on the lower surface only, they protrude below the lower epidermis very slightly (Pl. XXV, Fig. 11, is typical) and have no distinctive characters excepting in *europaeus nanus,* where all have their long axes more or less parallel with the midrib.

Trichomes are present in only three species; *alatus* has very few on the upper surface above the midrib, *americanus* has them on the upper epidermis above all the larger veins, and *atropurpureus* has them on the lower epidermis excepting along the veins.

The palisade layer is mostly two rows of cells high, although in *americanus* there is only one row, and in *patens* and *europaeus nanus* there are three rows, while in *alatus* it ranges between one, two and three cells in height. The palisade tissue makes up about

a third of the thickness of the leaf in *americanus* and *radicans*, about half in *atropurpureus, europaeus, bungeanus, patens, europaeus nanus* and *alatus*, and about two-thirds in *maakii*.

The spongy mesophyll is not distinctive excepting in *alatus*, where the lower layer is composed of very large, flattened, ameba-shaped cells which contain a substance that becomes somewhat salmon-colored when the leaves are cleared in chloral hydrate.

The midrib protrudes both above and below the leaf in all species excepting in *europaeus nanus*, and in *radiçans* only a little. In all, the vascular bundle is in the form of an arc, varying only in the extent that the arc is flattened. Bast fibers accompany the vascular bundle in *patens, americanus, radicans* and *alatus*, but are not present in the others. Parenchyma tissue surrounds the vascular bundles in all species excepting *alatus*, where all of the cells are more or less collenchyma. Assimilatory tissue, continuous with the palisade layer of the leaf blade, extends across the midrib in all species excepting *europaeus* and *bungeanus*. The cells of this tissue are rounded instead of elongate in all excepting *europaeus nanus*, where they are very similar to the palisade cells of the mesophyll. A layer of collenchyma tissue is just beneath the epidermis on both the upper and lower surface of the midrib in all species excepting *europaeus nanus*. In *patens* and *radicans* this layer is very thin.

The lateral veins are connected with both upper and lower surfaces by more or less collenchymatous cells in *atropurpureus, europaeus, maackii* and *alatus*, connected to the lower surface by collenchyma but immersed above in *bungeanus* and *americanus*, and completely immersed in *patens, europaeus nanus* and *radicans*, although in *radicans* the sheath around the bundle extends to within about one cell layer of the epidermis. Bast fibers accompany the lateral veins in *patens, europaeus nanus* and *alatus*, but not in the others.

## GENERAL SUMMARY.

The descriptions of the stem are based on studies of the fifth or sixth internode from the terminal bud-scale scars of the second year of growth, with supplementary studies of the fourth or fifth internode of the present year's growth.

The outer wall of the epidermis of the stem is rather thick; in only two species, *atropurpureus* and *maackii*, is it less than half of the thickness of the radial diameter of the epidermal cells. The epidermis is quite persistent, being still present in places on stems

three to six or seven, or even more, years of age. It is usually but one cell in thickness.

Cork begins its formation in all species in either the first or second year, either as lines or wings at or between the corners of the stem or as small flecks which resemble lenticels scattered promiscuously over the stem. The so-called wings of *atropurpureus, europaeus,* and *bungeanus* are not *homologous* with the wings of *alatus,* either in the method of their origin, the general appearance of their cells, or their location on the stem. The cork is formed both from cells cut off from the epidermal cells and from the collenchyma cells beneath the epidermis.

Two cylinders of collenchyma tissue in the outer cortex, separated from each other by a layer of assimilatory tissue, is characteristic of the genus. The outer cylinder is just beneath the epidermis and is composed of colorless cells. The inner may or may not contain some chloroplasts. In some species the two cylinders are connected by collenchyma cells cutting through the assimilatory tissue at the corners of the stem. The inner layer of collenchyma is more variable than the outer in its prominence, the thickness of the cell walls, etc.

The assimilatory tissue present in the cortex of all species is from three to six cells in thickness. The cells in some species are palisade-like in arrangement, in others the long axis of the cells is in the direction of the circumference of the stem.

Between the inner layer of collenchyma and the phloëm is a layer of thin-walled parenchyma cells.

Bundles of bast fibers are found just outside of the assimilatory tissues at the corners of the stem in *atropurpureus* and *europaeus,* and just inside of the assimilatory tissue in *americanus.* Scattered fibers, singly or in groups of two or three, are present just outside of the phloëm in *atropurpureus, europaeus, bungeanus* and *americanus.*

Tracheal tubes, tracheids, wood fibers and wood parenchyma are all found in the xylem throughout the genus. The wood parenchyma is scarce, the cells are rather short and blunt and thin-walled as compared with the other elements. The borders of the pits of the tracheids are very narrow, making them very difficult to recognize. The cells are about the size and shape of the wood fibers. Solereder states that the tracheids are more abundant than the wood fibers. My observations have led me to believe that just the reverse is true.

The medullary rays may be considered as one cell thick throughout the genus. In some species the long axis of these cells is in the

radial direction, in some it is in the vertical direction, and in still others long axes are found in both directions.

The cells of the pith are somewhat elongated vertically and are rounded in cross section. The pith varies with the species. In some it is empty, in others homogeneous and filled with starch, while in others it is heterogeneous, consisting of both living and dead cells.

In the petiole the vascular bundle in all species is an arc, although in *alatus* the xylem is more extended, making the bundle more fan-shaped. The ends of the arc in a few species bend sharply inward. In some species small cylinderical bundles occur just outside of the main bundle. In *atropurpureus* these small bundles have phloëm completely surrounding the xylem, but in the others this is not the case.

Bast fibers were not found in the petioles of any of the species studied. Stenzel reports bast fibers in the petiole of *europaeus*, but after repeated search I failed to find any in the materials used for this study.

Outside of the vascular bundle, the remainder of the petiole is composed of parenchyma and collenchyma cells, the collenchyma being constant for all species in the region just beneath the epidermis. The collenchyma and also the parenchyma cells are pitted in some species.

The upper surface of the petiole varies among the different species, and although the variations are probably dependent on the variations in the length of the petiole itself, they nevertheless seem constant enough in the species to be of systematic value. The margins project above the upper surface in some species, notably so in *atropurpureus*, in others the margins are completely rounded. The upper surface is concave in some species, flat in *europaeus nanus*, and convex in other species. Trichomes are present in *alatus* and *americanus*, although quite rarely in the former.

The epidermal cells of the leaf are always broader than tall. The outer walls are not greatly thickened, and for the most part vary from flat to slightly bulged outward, a variation which, like the variations from straight to curved or sinuous of the side walls, could be dependent on the amount of turgidity of the cells. Only in *europaeus nanus* was the bulging a noticeable natural character of the cells. The side walls of the cells of the upper epidermis in all species studied were pitted, although in some the pits were very

fine. Those of the lower epidermis varied in this regard. In some they were pitted, while in others they were not.

Stomata were found on the under side of the leaves only.

Trichomes are present on the under surface of the leaf in *atropurpureus,* and along the veins on the upper surface in *alatus* and *americanus.*

The palisade layer is mostly two-rowed, although in one species it is only one row high and in others it is three rows. For the most part this layer makes up about one-half of the thickness of the leaf, but in *maackii* it occupies two-thirds of the thickness, while in *americanus* and *radicans* it occupies only one-third.

Collenchyma tissue is quite prominent in the midrib of most of the species studied. Bast fibers accompany the midrib and lateral veins in some species, but not in others. The lateral veins connect with both surfaces of the leaf by collenchyma cells in some species; with only one surface, the vein being immersed on the other side, in other species, while in still others it is completely immersed.

Concerning the effects of geographical isolation, it does not seem possible to attribute the variations found between the species studied to this cause, nor do those species found in comparative proximity seem to show greater likenesses to each other than to other species widely separated from them. *Patens* is a native of China and *radicans* a native of Japan and Korea. The former is a recumbent shrub while the latter is a trailing or climbing vine. These two species have a number of systematically important characters in which they do agree. *Alatus,* a native of Japan, Korea, China and Manchuria, stands out distinctly different from all other species. Further, *europaeus,* native of Europe, *atropurpureus* of North America and *maackii* of Korea, Manchuria and China, are much alike in many characters. *Bungeanus,* a native of China and Manchuria, strongly resembles *americanus* in some characters and *europaeus* in others.

KEY TO SPECIES BASED ON THE CHARACTERS OF THE STEM.

I. Collenchymatic cylinders connected at the corners of the stem.
  1. Outer collenchymatic cylinder more than one cell thick.
    A. Bast fibers in the cortex, at the corners very weakly developed cork wings which are soon sloughed off.
      a. Bundles of fibers at the corners just beneath the outer collenchymatic cylinder. Empty pith.
        (1) Assimilatory tissue cells with long axis in tangential direction, medullary-ray cells with long axes in their radial diameter. Outer wall more than half as thick as radial diameter of epidermal cells.....*E. europaeus.*

(2) Assimilatory tissue cells with long axis not in tangential direction, medullary ray cells—some with long axis in vertical and others in radial diameter. Outer walls less than half as thick as the radial diameter of the epidermal cells. *E. atropurpureus.*

b. No bundles of bast fibers present. Pith is heterogeneous.

(1) Assimilatory tissue with the long axis of the cells in tangential direction. Medullary-ray cells with long axes in radial direction. Outer wall more than half as thick as radial diameter of epidermal cells.....*E. bungeanus.*

B. No bast fibers in the cortex. No corkwings.

a. Heterogeneous pith.

(1) Assimilatory tissue with long axes of cells in tangential direction. Medullary-ray cells with long axes in vertical direction. Outer wall more than half as thick as the radial diameter of the epidermal cells.....*E. maackii.*

II. Collenchyma cylinders not connected at the corners.

1. Outer collenchyma cylinder more than one cell thick.

A. No bast fibers in the cortex. Well-developed cork wings between the corners of the stem.

a. Empty pith.

(1) Assimilatory tissue cells with long axis in radial diameter. Medullary-ray cells with long axes in their radial direction. Outer wall thicker than the radial diameter of the epidermal cells .....*E. alatus.*

2. Outer collenchyma cylinder one cell thick.

A. Bast fibers in the cortex. Corkwings not present at the corners of stem.

a. Bundles of fibers at the corners of the stem inside of the assimilatory tissue. Heterogeneous pith.

(1) Assimilatory tissue with long axes of the cells in radial diameter. Medullary-ray cells with long axes in vertical direction. Outer wall thicker than radial diameter of the epidermal cells.....*E. americanus.*

B. No bast fibers in the cortex. Cork wings not present at the corners of the stem.

a. Pith homogeneous. Medullary-ray cells with long axis in vertical direction.

(1) Assimilatory tissue cells with long axis in radial diameter. Outer wall more than half the radial diameter of the epidermal cells.

*. Assimilatory tissue palisadelike entirely around the stem. Epidermis one to two cells thick, cells of fairly uniform shape and size.....*E. patens.*

†. Assimilatory tissue palisadelike on one side of the stem, irregular on the other. Epidermis one cell thick; large cells occur at short intervals, throwing the epidermis into small peaks.....*E. radicans.*

(2) Assimilatory tissue cells with long axes not in radial diameter. Outer wall more than half the radial diameter of the epidermal cells. Epidermis one cell thick. *E. europaeus nanus.*

## KEY TO SPECIES BASED ON THE CHARACTERS OF THE PETIOLE.

I. Margins project above upper level of petiole.
  1. Upper surface of petiole convex.
    A. Collenchyma around outer margin pitted.
      a. Fine pits.
        (1) Vascular bundle an arc, ends bend sharply in.
          *. Accessory vascular bundles (closed bundles) near ends of the arc. Parenchyma outside of the vascular bundle thin-walled with fine pits.....*E. atropurpureus.*
          †. No accessory vascular bundles. Parenchyma outside of the vascular bundle thin-walled with no pits. *E. maackii.*
    B. Collenchyma around outer margin not pitted.
        (1) Vascular bundle an arc, ends bent sharply in.
          *. Accessory vascular bundle (open bundles) near ends of the arc. Parenchyma outside of vascular bundle thin-walled; no pits.....*E. europaeus.*
        (2) Vascular bundle fan shaped.
          *. No accessory vascular bundles. Very thick-walled collenchyma instead of parenchyma outside of vascular bundle; no pits. Scattered trichomes on upper surface. *E. alatus.*
  2. Upper surface of petiole concave.
    A. Collenchyma around outer margin pitted.
      a. Prominent pits.
        (1) Vascular bundle an arc, ends not bent in.
          *. No accessory bundles. Parenchyma outside of vascular bundle thin-walled, fine pits.....*E. bungeanus.*

II Without margins projecting above upper level of petiole.
  1. Upper surface of petiole convex.
  2. Upper surface of petiole concave.
    A. Collenchyma around outer margin pitted.
      a. Prominent pits.
        (1) Vascular bundle an arc; ends not bent in.
          *. No accessory vascular bundles; parenchyma outside of vascular bundle thick-walled with prominent pits.
            o. Irregularities in epidermis but no trichomes.
              ‡. Arc of the vascular bundle greatly flattened; only the ends are curved. Middle third of the upper surface concave, outer thirds strongly convex. *E. patens.*
              §. Collenchyma layers around outer margin only one to two cells thick.....*E. radicans.*
            oo. Trichomes present.....*E. americanus.*
  3. Upper surface of petiole flat.
    A. Collenchyma around outer margin pitted.
      a. Prominent pits. (Only the outer and inner walls of these collenchyma cells are thickened.)
        (1) Vascular bundle an arc; ends not bent in.
          *. No accessory bundles. Parenchyma outside of the vascular bundle thin-walled with no pits. *E. europaeus nanus.*

## KEY TO SPECIES BASED ON THE CHARACTERS OF THE LEAF BLADE.

I. Bast fibers in the midrib.
  1. Bast fibers in lateral veins.
    A. Lateral veins immersed. Three rows of palisade cells. Side walls of both upper and lower epidermis pitted. No trichomes. *E. patens.*
    B. Lateral veins immersed on upper side; on under side extending through by collenchyma tissue. One row of palisade cells. Side walls of both upper and lower epidermis pitted. Trichomes on upper epidermis above all larger veins..... *E. americanus.*
    C. Lateral veins extending from surface to surface by means of collenchyma tissue. One-two-three rows of irregular palisade cells. Side walls of upper epidermis finely pitted, of lower may or may not be pitted. Scattered trichomes above midrib.....*E. alatus.*
  2. No bast fibers in lateral veins.
    A. Lateral veins immersed (collenchyma cells around these veins almost through the leaf above and below.) Two rows of palisade cells. Side walls of both upper and lower epidermis prominently pitted. No trichomes.....*E. radicans.*

II. No bast fibers in midrib or lateral veins.
  A. Lateral veins immersed. Three rows of palisade cells. Side walls of both upper and lower epidermis pitted (long oval pits). No trichomes. No collenchyma in the midrib...*E. europaeus nanus.*
  B. Lateral veins immersed on upper side; on under side extending through by collenchyma tissue. Two rows of palisade cells. Side walls of both upper and lower epidermis finely pitted. No trichomes .....*E. bungeanus.*
  C. Lateral veins extending from surface to surface by means of collenchyma tissue. Two rows of palisade cells. Side walls of upper epidermis pitted, of lower not pitted.
    a. Trichomes on lower surface of the leaf....*E. atropurpureus.*
    b. No trichomes.
      (1) Cells of the upper epidermis very large, of the lower epidermis rather sinuous. Palisade cells very loosely arranged; occupy two-thirds of thickness of leaf. *E. maackii.*
      (2) Cells of upper epidermis moderate in size, of lower epidermis sides rounded but not sinuous. Palisade cells compactly arranged; occupy one-half of thickness of leaf. *E. europaeus.*

## ACKNOWLEDGMENT.

This work was done in the botany laboratories of the University of Kansas under the direction of Prof. W. C. Stevens. It is with a deep sense of obligation that I wish to express my sincere appreciation to Professor Stevens for many helpful suggestions and for his continuous interest throughout the time that the work was in progress.

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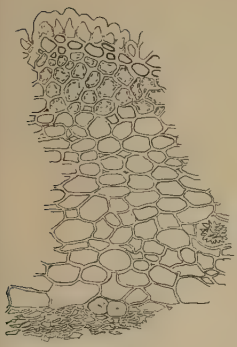
## PLATE XXII.

FIGS. 1 TO 9.—Cross sections through the cortex of two-year-old stems.
1, *E. atropurpureus;* 2, *europæus;* 3, *E. bungeanus;* 4, *E. maackii;* 5, *E. patens;* 6, *E. americanus;* 7, *E. europæus nanus;* 8, *E. radicans;* 9, *alatus.*

PLATE XXII.



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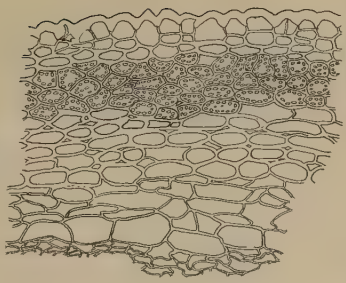

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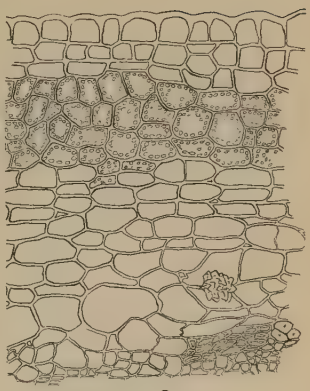

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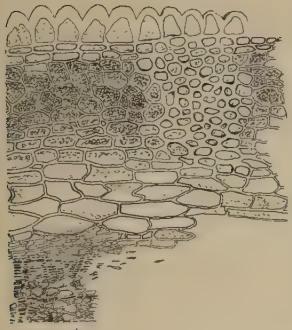

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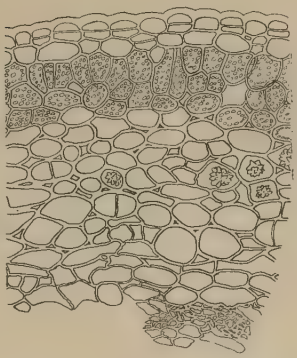

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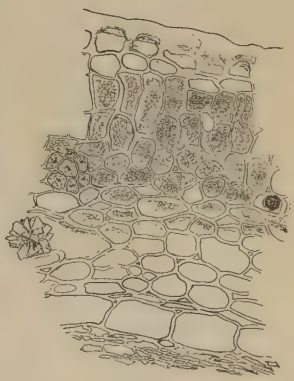

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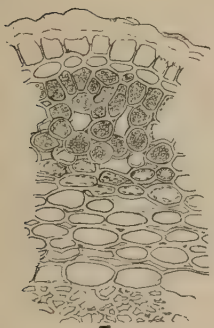

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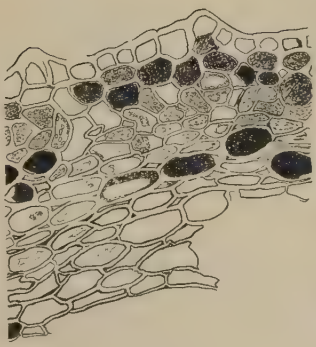

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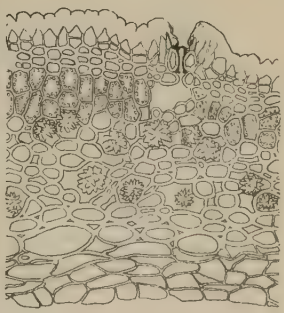

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## PLATE XXIII.

FIGS. 1 TO 9.—Semidiagrammatic cross sections through one-year-old stem: 1, *E. atropurpureus;* 2, *E. europæus;* 3, *E. bungeanus;* 4, *E. maackii;* 5, *E patens;* 6, *E. americanus;* 7, *E. europæus nanus;* 8, *E. radicans;* 9, *E. alatus.*

FIG. 10.—*E. atropurpureus.* Origin of bast fibers in cortex of two-year-old stem.

FIG. 11.—*E. atropurpureus.* Collenchymatic origin of cork.

FIG. 12.—*E. atropurpureus.* Cork formation cutting out bundle of bast fibers at corner of stem.

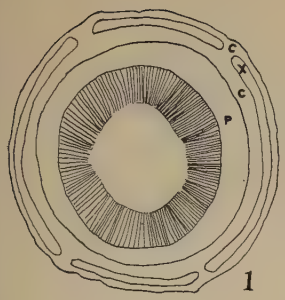
FIG. 13.—E. *atropurpureus.* Drawing of the stem to show the location of the first cork lines.

FIG. 14.—*E. patens.* To show enlarged collenchymatic cell at A.

ABBREVIATIONS ON PLATE.

*B,* cork; *C,* collenchyma; *X,* assimilatory tissue; *P,* parenchyma (thin-walled).

PLATE XXIII.



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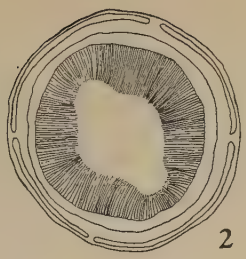
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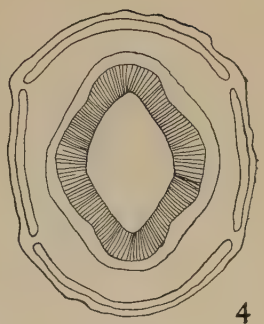
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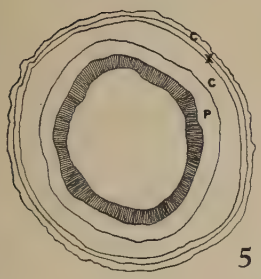

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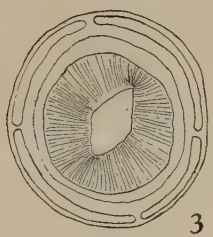
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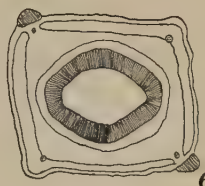
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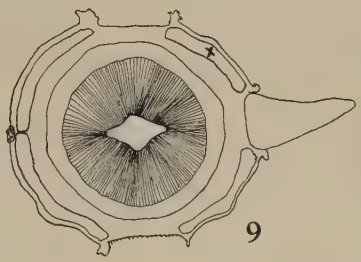
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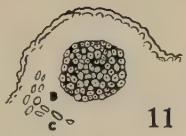

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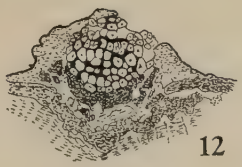
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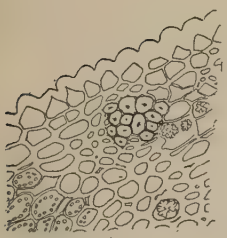
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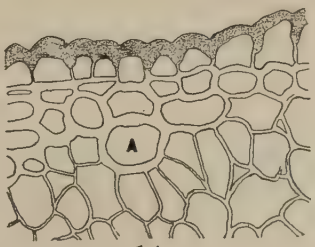
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## PLATE XXIV.

FIG. 1.—*E. americanus.* Collenchymatic origin of cork.

FIG. 2.—*E. europœus nanus.* Epidermal origin of cork in one of the lenticel-like cork warts.

FIG. 3.—*E. europœus nanus.* Cross section of thick-walled parenchyma tubes just outside of the phloëm.

FIG. 4.—*E. alatus.* Epidermal origin of cork wing.

FIG. 5.—*E. alatus.* Cork cells from the wing.

FIGS. 6 TO 15.—Portions of medullary rays drawn from radial sections:

6, *E. atropurpureus;* 7, *E. europœus;* 8, *E. bungeanus;* 9, *E. maackii;* 10, *E. patens;* 11, *E. americanus;* 12, *E. europœus nanus;* 13, *E. europœus nanus,* tangential section; 14, *E. radicans;* 15, *E. alatus.*

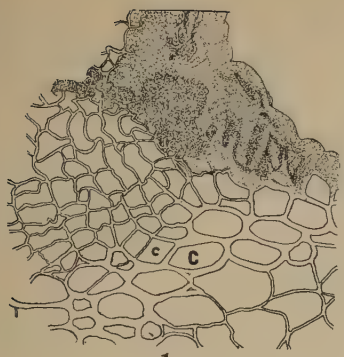
FIGS. 16 TO 24.—Semidiagrammatic cross sections through the midrib of the leaves.

16, *E. atropurpureus;* 17, *E. europœus;* 18, *E. bungeanus;* 19, *E. maackii,* 20, *E. patens;* 21, *E. americanus;* 22, *E. europœus nanus;* 23, *E. radicans;* 24, *E. alatus.*

ABBREVIATIONS ON PLATE.

*C,* collenchyma; *B,* bast fibers; *X,* assimilatory tissue; *S,* sclerenchyma cells; *P.* thin-walled parenchyma.

PLATE XXIV.

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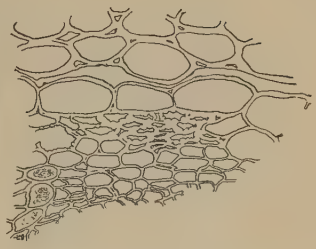

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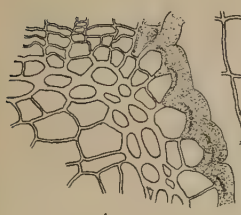

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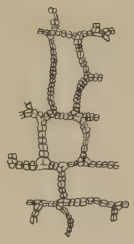

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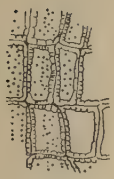

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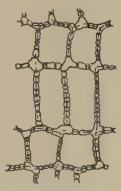

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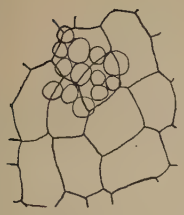
## PLATE XXV.

Surface views of the upper and the lower epidermis of the leaves. The palisade cells are shown beneath the upper epidermis.

FIGS. 1 AND 2.—*E. atropurpureus.*
FIGS. 3 AND 4.—*E. europœus.*
FIGS. 5 AND 6.—*E. bungeanus.*
FIGS. 7 AND 8.—*E. maackii.*
FIGS. 9 AND 10.—*E. patens.*
FIG. 11.—Stoma from *E. patens.*
FIGS. 12 AND 13.—*E. americanus.*
FIG. 14.—Trichome from the epidermis of *E. americanus.*
FIGS. 15 AND 16.—*E. europœus nanus.*
FIGS 17 AND 18.—*E. radicans.*
FIGS. 19 AND 20.—*E. alatus.*
FIG. 21.—*E. alatus.* Lower layer of spongy mesophyll as seen through the epidermis.

PLATE XXV.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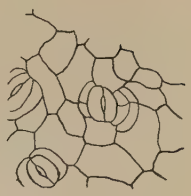
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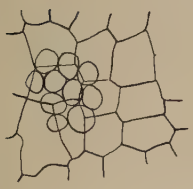
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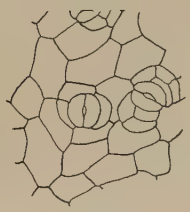
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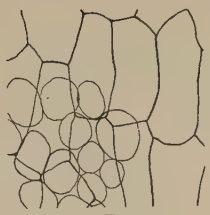
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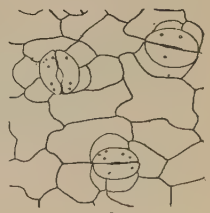
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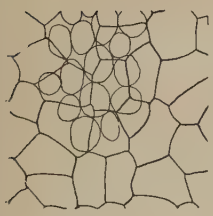
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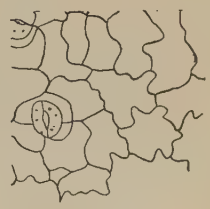
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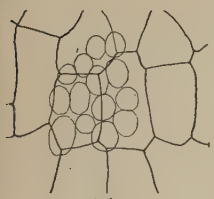
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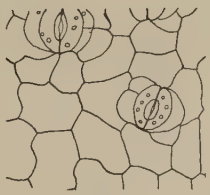
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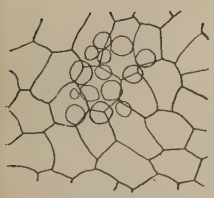
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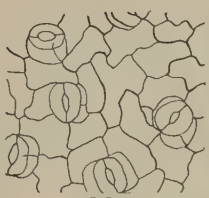
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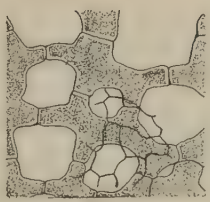
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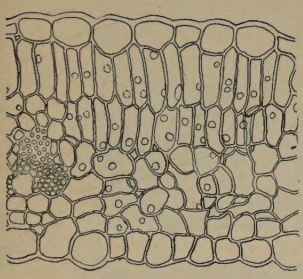
## PLATE XXVI.

Cross sections through the leaves

FIG. 1.—E. *atropurpureus.*
FIG. 2.—*E. europæus.*
FIG. 3.—*E. bungeanus.*
FIG. 4.—*E. maackii.*
FIG. 5.—*E. patens.*
FIG. 6.—*E. americanus*
FIG. 7.—*E. europæus nanus.*
FIG. 8.—*E. radicans.*
FIG. 9.—*E. alatus.*

PLATE XXVI.



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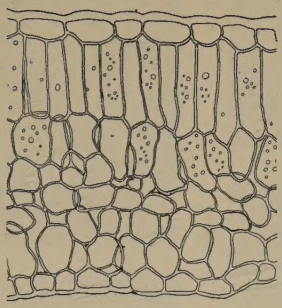

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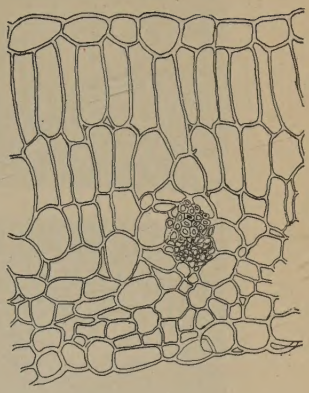

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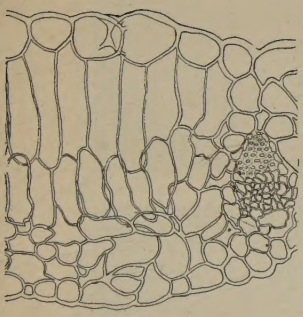

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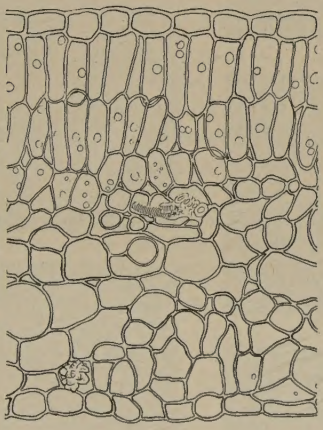

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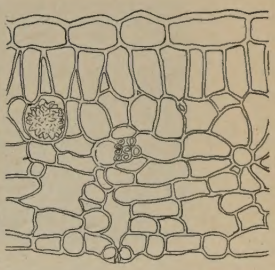

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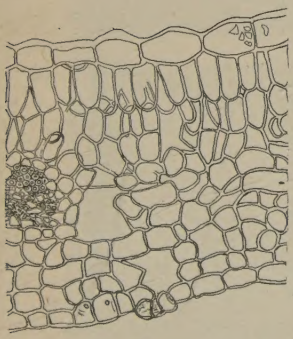

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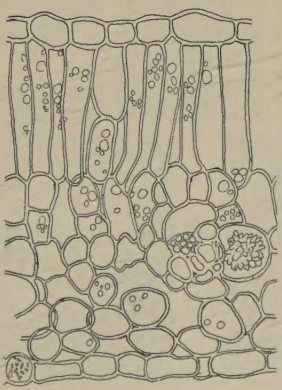

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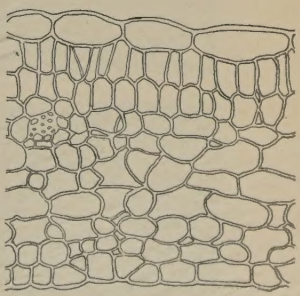

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## PLATE XXVII.

Microphotographs of petioles.

FIG. 1.—*E. atropurpureus.*
FIG. 2.—*E. europæus.*
FIG. 3.—*E. bungeanus.*
FIG. 4.—*E. maackii.*
FIG. 5.—*E. patens.*
FIG. 6.—*E. americanus.*
FIG. 7.—*E. europæus naus.*
FIG. 8.—*E. europæus nanus,* enlarged.
FIG. 9.—*E. radicans*
FIG. 10.—*E. alatus.*
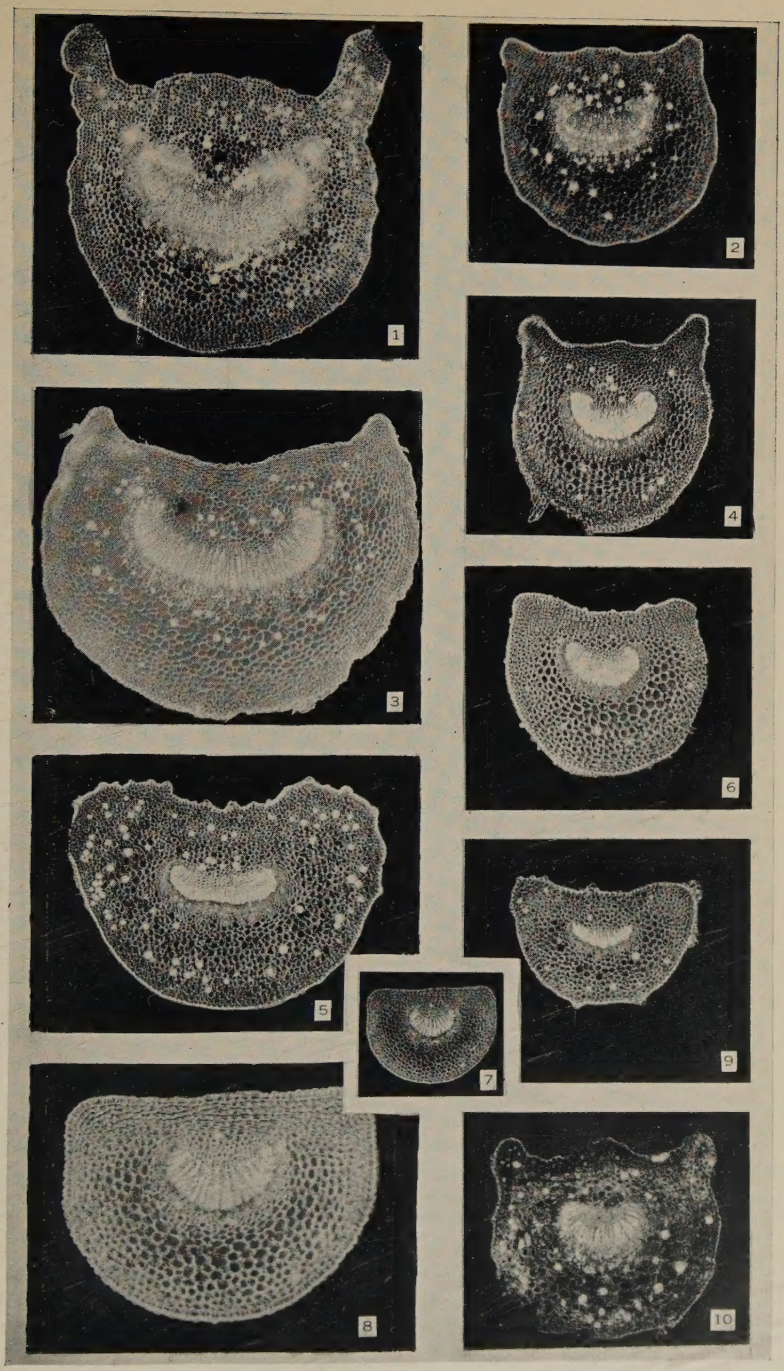
PLATE XXVII.